SOME CONTRIBUTIONS TO MOORLAND ANT ECOLOGY

D. A. MUIR

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Contents

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1.1 Introduction

The study of natural communities of organisms may be divided conveniently (although artificially) into several categories which are analogous to certain of the major divisions of Biology as a whole (Park, 1941). Communities may be classified and arranged in different groups and sub-groups according to their structure and morphology. This is the taxonomic aspect, and has been the main field of ecological expansion to date. Allied to the study of community type is that of the causes and results of change from one type to another, i.e. the genetics and evolution of the community. Finally the functional aspect, the integration of the community may be considered, or, in pursuance of the analogy, its physiology.

It was with the latter category that the present series of observations were mainly concerned. Attention was confined to part of a community only, but an important, well defined and relatively complex part, namely the ant fauna.

Elton's (1949) plea for a broader approach by animal ecologists pointed out the need for co-ordination of ecological observations and the fitting of the latter into a perspective of the ecosystem as a whole. Cragg (1961) approves of this aim, and inclines to the view that the objective may best be reached by synthesis of carefully chosen basic researches, provided that these are carried out with the question "What are the functions of these organisms in the biological history of moorland?" firmly borne in mind. The latter author also emphasises the importance of listing not merely the species of animals which

may occur together in a limited area, but also their physical and biotic needs (and, we may add, their physical and biotic capabilities) which are responsible for their occurrence together.

The area where most of the field investigations were carried out lay between the villages of Renton and Cardross in West Dunbartonshire (National Grid Ref. 26/369784) and at an altitude of just over five hundred feet. Geologically, it was based on Upper Old Red Sandstone, the rock type (which was near the top of the series stratigraphically) being a well-cemented sandstone with occasional beds of gritty material approaching an arkose in composition. The strata had a dip of thirty degrees to the South-East. Igneous intrusions were represented by a dolerite dyke and a sill of marlie basalt which were very near the experimental sites, although not actually running through them. Differential erosion of the rocks noted above had resulted in a topography in which the main features were a series of sandstone ridges striking North-East to South-West. There was a thin veneer of glacial drift in low-lying pockets.

The area being described was not part of the main grouse-moor, and was, in consequence, burnt very irregularly, the main component of the vegetation being Callunetum of about twelve years' standing. Sheep, and occasionally cattle, had access to the area however, and together with rabbits (Oryctolagus cuniculus) and hares (Lepus europaeus) maintained several small areas of Agrostis/Festuca plagioclimax along the sandstone ridges. Also present in the plagioclimax vegetation were sheep's sorrel (Rumex acetosella), tormentil (Potentilla erecta), heath bedstraw (Galium saxatile) and a sedge (Carex sp.). Occurring in the Callunetum, mainly along the drainage runnels, were blue moorgrass

(Molinia coerulea), cotton sedge (Eriophorum vaginatum), cross-leaved heath (Erica tetralix), sundew (Drosera rotundifolia), butterwort (Pinguicula vulgaris) and Sphagnum spp. with Juncus squarrosus in the damper patches.

The vertebrate fauna, besides those animals already noted as playing the most important part in the maintenance of the biotic plagioclimax, included red grouse (Lagopus lagopus scoticus), kestrel (Falco tinnunculus), meadow-pipit (Anthus pratensis), curlew (Numenius arquata), lapwing (Vanellus vanellus), stoat (Mustela erminea), field vole (Microtus agrestis), pigmy shrew (Sorex minutus), frog (Rana temporaria) and toad (Bufo bufo).

The invertebrate fauna was too large to enumerate here, and it may suffice to point out that it contained no unusual features. Cercopids, collembola and coccids were abundant. The ant species represented were:-

Myrmica rubra L.

Myrmica scabrinodis Nylander

Formica lemani Bondroit

Leptothorax acervorum F.

Of the above, only the first three species were present in large numbers, and it is on these that emphasis was placed in the investigations.

Where two or more similar species co-exist in the same community at least some of their requirements, whether those be food, shelter or tolerated range of microclimate etc., must be different to some degree (Park, 1944). The less these requirements overlap in space, time and materials the more advantageous it is for the species concerned, and the more economic is the coverage of the available resources from their

point of view. It was hoped to find out some of the ways in which the above ecological principle might apply to the ants of this moorland community, and to elucidate any eco-differentiating characteristics of the various species.

Some of these possible characteristics were sought for under five main headings (Items 2 to 6 inclusive). Item 7 is included by way of illustration of how even such a factor as differing mineral composition of different rock-types may offer a variety of microclimatic niche which, in turn, provides scope for eco-differentiation.

M.V.Brian and H.Talbot are the principal workers who have dealt with the same,or closely related, ant species as those which are considered here.

2. Nest-Site Association and Stability

2.1 Introduction

In this phase of the study the nesting attractiveness of an area of Agrostis/Festuca plagioclimax was increased with a view to investigating the dynamics and stability of any resulting colonisation by the various ant species.

The two major physical factors controlling ant colonisation in this area were:

(a) Degree of trampling by grazing animals and

(b) Availability of insolation.

The obstacles encountered by Formica and Myrmica in the colonisation of a relatively bare piece of plagioclimax such as this are similar insofar as the trampling by grazing animals is concerned. Formica lemani, however, suffers from the additional disadvantage of apparently requiring a solid roof in its nest architecture, and one exposed to a high degree of insolation, whereas the two Myrmica species are quite able to build up into an area of insolation by their own efforts, and consequently may colonise turf provided the grass is not too long. It is possible that the much stouter integument of the myrmecines (Page 62) may have some significance in the development of this ability to dispense with a solid cover to the nest.

The importance of adequate insolation for the

maintenance and continued growth of ant colonies has been investigated by Brian and Brian (1951) who demonstrate the various inter-related factors, dependent on solar radiation, which influence the life of a colony.

A situation was selected for this particular experimental series which possessed the following characteristics, viz:- An area of Agrostis/Festuca plagioclimax with Potentilla erecta, Rumex acetosella and a little Juncus communis associated. This was situated on the dip slope of one of the ridges already described, and was therefore sheltered from the North and had a gentle southerly aspect. It was bounded to the North and South by Calluneturn of about twelve years' standing as the area was not part of the main grouse-moor and was not regularly keepered. Laterally, the site selected was joined to similar clearings by grassy sheep-tracks. The insect fauna was abundant. All four ant species were represented, but the number of nests was small as there were very few protected sites in this particular clearing, and the formation of turf nests by the myrmecines was discouraged by the trampling of sheep and occasional cattle which, together with hares and rabbits, maintained the plagioclimax. The locality chosen is shown in Plate 1.

The radiation-absorbing capacity of a given piece of ground is affected by:-

(a) Material of surface exposed to insolation
(b) Colour of surface exposed to insolation
(c) Texture of surface exposed to insolation
(d) Topography of surface exposed to insolation

(Geiger, 1957).

Factors (c) and (d) are important only in extreme

cases, and then the effect is most marked when the incident radiation is at a low angle. The main factors controlling energy absorption are the material exposed and its colour. It was decided that the most natural method of increasing the absorptivity of the soil surface in the area would be by placing stones on the surface of the quite short grass. This was similar to the method used by Brian (1952a).

It was also decided to combine this general colonisation experiment with an investigation of the effect (if any) that potential nest sites of different rock-types might have on the population distribution, i.e. an attempt to detect any possible differential colonisation (due either to specific preferences or general preference) on account of the differing thermal properties of the rock-types used. The study of the influence of the geological substrate on the microclimatic complex of any given area is one which appears to have received little attention in ecological investigations. Its effect will be most marked in areas where the bedrock is near the surface, and, to a lesser extent, in non-glaciated districts where the soil is in situ. Glacial drift soils, which normally consist of rock debris of widely differing origins, present a potentially more complex microclimatic mosaic.

A proper investigation of the influence of stratigraphy on microclimate would encroach on the bounds of physical geology and meteorology, and lies outside the scope of the present investigations. The subject is mentioned merely in explanation of the bearing which the additional facet of the proposed observations has on moorland ant ecology. We are not

concerned at present with the heat economy of a large district, but only the diurnal thermal effects of different rock-types in a small area with a uniform bedrock and herb cover, in short, this approaches the conditions of the glacial drift soil surface so characteristic of most Scottish Midland areas.

2.2 Method

In accordance with the aims described above, three rock-types which were representative of the three main petrological systems (i.e. sedimentary, igneous and metamorphic) were selected for use as potential nest sites. These rock-types were:-

(a) Upper Old Red Sandstone, from near the top of the series.

(b) Markle basalt, intrusive as a sill in the area.

(c) Luss slate.

The rocks were trimmed to the following dimensions:-

Sandstone and basalt: 15 X 10 X 5 cms.

Slate : 15 X 10 X 1 cms.

Twenty-seven units of each type were made, and laid out as follows:

(i) Three quadrats, each of sixteen units, and each consisting of one of the above rock-types , were laid with 15 cms between the units. The three quadrats were laid with as identical an aspect as possible, and one metre apart.

(ii) Eleven "triplets" were laid, each consisting of three units (one of each rock-type) in mutual contact. These were placed at random in the experimental area.

There were thus eighty-one potential nest-sites provided in this way.

A further thirty sandstone units, each of approximately 20 cms square and 5 cms thick, were trimmed and laid in a rectangle of 3 by 10 units with 4 cms between units. This quadrat was placed in an area of plagioclimax very similar to the main area and 15 metres distant from it. The latter quadrat thus gave a very closely knit insolation area and was designed for comparison with the more dilute sandstone element in the main area.

The above new potential nest-sites were all placed in position during the last week in July, 1952, and were disturbed as little as possible thereafter, apart from checking and adjustment of any units which were displaced by sheep.

2.3 Results

The potential nest-sites, provided as described above, were examined on the following dates:-

6 August 1952
4 July 1953
25 September 1953
27 April 1954
18 July 1954
18 September 1956

(The 1956 observations were made when the author re-visited the district after an absence of two years. As some of the quadrats had been slightly disturbed during this interval the final nest count is not strictly comparable with the rest. It is, nevertheless, a good approximation, and is presented as providing an indication of the continued population trend).

The number of units colonised, by each species and in

total, in the main experimental area on each of the above dates is presented in Figures 1 to 13 inclusive. In view of the compact nature of the "triplets", where the three constituent units were mutually in contact, Fig. 3 has been drawn where each "triplet" is considered as one unit. This is to allow for any polydomous tendencies on the part of any of the species (especially F.lemani) and to give a truer nest population picture as distinct from the rock-preference aspect. The latter, i.e. the comparative colonisation of the three different rock-types provided, is presented in Figures 15 to 19 inclusive. Figure 14 shows the results for the large compact sandstone quadrat.

We may now consider the results in detail:-

(a) Sandstone Quadrat (open). Figs. 1 and 1a.

After a steep initial rise due to immigration of F.lemani and M.scabrinodis, the percentage curve settles to a steady climb until the 80% level is reached in July 1954. When examined in 1956 the percentage was found to be unaltered, although the population composition had altered slightly - M.scabrinodis having increased by one unit and L.acervorum having decreased by the same amount. M.ruber was not observed in this quadrat. (For a discussion of the more compact sandstone quadrat please see Page 16).

(b) Basalt Quadrat. Figs. 2 and 2a.

No colonisation took place in the year of laying, and was at a very low level until the middle of 1954. Between 1954 and 1956 (by which time the quadrat was still less than 50% colonised), a slight increase of all species (with the exception of M.ruber which was never represented) took place.

(c) Slate Quadrat. Figs. 3 and 3a.

Here a slow but steady increase is seen, due mainly to F.lemani. M.rubra appears only in the late 1953 and early 1954 readings, and L.acervorum only in late 1954 and 1956. M.scabrinodis was never recorded.

(d) Triplet Sandstone. Figs. 4 and 4a.

Colony increase is slightly more irregular than in the open sandstone quadrat, due to fluctuation of L.acervorum and M.rubra. It does, however, rise to the same percentage as the open sandstone quadrat in 1956.

(e) Triplet Basalt. Figs. 5 and 5a.

Here colonisation was much heavier than in the basalt quadrat (possibly due to the proximity of the other rock-types), with a high initial immigration figure followed by somewhat irregular colony growth due to fluctuation of F.lemani and M.rubra. The 1956 figures show a slight decline in M.scabrinodis and F.lemani.

(f) Triplet Slate. Figs. 6 and 6a.

In contrast to the slate quadrat, a rapid colonisation took place (again due mainly to F.lemani), and by the middle of 1955 all but three slate units had been occupied. The unoccupied units were those whose adjoining sandstone and basalt units were colonised by myrmecines. This explains the plateau at 73% on the colonisation curve which continues till the last 1954 reading. The F.lemani curve in Fig.6 shows a corresponding plateau, suggesting inability on the part of the latter species to gain a foothold in "triplets" where myrmecines control two of the three units. By early 1954 every "triplet" had been occupied to some extent, and Figs. 8 and 8a show the position when each triplet is considered as an indivisible unit. The 1956 readings

show a great decrease in slate units colonised. This was due to destruction by weathering and displacement over the preceeding two years, and consequent reduction in the number of units available. This also occurred in the slate quadrat, but to a lesser extent, the debris there being consolidated by the herb cover and no displacement having taken place. M.scabrinodis did not occupy slate units.

(g) Total Sandstone, Total Basalt and Total Slate.

Figs. 10,10a; 11,11a; 12,12a.

The colonisation situation for each rock-type is shown here, the quadrat and triplet results being combined. By 1954 the available sandstone units had been 74% colonised, basalt and slate being at the same level of 48%. The 1956 figures show more of a scatter, the sandstone now being 80% colonised, basalt 60% colonised and slate showing a slight decline to 44% due to reasons discussed above.

(h) Quadrat Totals and Triplet Totals. Figs. 7,7a; 9,9a.

These afford a comparison between the colonisation rates in the quadrats on the one hand and the triplets on the other. Although the triplet percentage curve reaches a higher figure (75%) in 1954, its climb is more erratic than that of the quadrats which reaches a level of 44%. The 1956 triplet reading shows a decline to 54% of the original availability (again due mainly to disintegration of the slate units), while the quadrats climb to 67%.

(i) Grand Total (81 units). Figs. 13 and 13a.

These show the combined results for the main observation area. The typical initial immigration and continued high colonisation rate of F.lemanii is especially well brought out. The only species displaying an overall fluctuation is M.rubra.

2.4 Discussion

2.4.1 General population increase and stability.

2.4.2 Effect of dilution of insolation surface.

2.4.3 Distribution of the various species among the three different rock-types.

2.4.1 General population increase and stability:

The importance of insolation in the distribution and internal economy of ant colonies has been demonstrated by Brian and Brian (1951), Gosswald (1932, 1938, 1941), Steiner (1929) and Talbot (1934). Brian and Brian, by studies conducted in heather and woodland subseres in the West of Scotland, have shown that insolation and its ancillary factors affect colony size and worker size besides interspecific distribution (F.lemani was the first species to vanish on the encroachment of the plant cover). Brian (1952a) also demonstrated that M.scabrinodis has a greater site tenacity than M.rubra. Although the observations being described here took place in conditions of biotic plagioclimax, and at a greater altitude, there are evidently certain principles still in operation.

As can be seen from Figures 1 to 12, F.lemani showed the greatest initiative and continued drive in the colonisation of the new insolation sites presented. This is summarised in Fig. 13. This feature was due, perhaps, to the greater mobility of F.lemani relative to that of the other species (Page 32) and is demonstrated by the steep rise of the F.lemani population curve during the first week of colonisation when immigration was the only effective means of population increase in the experimental area.

Considering all experimental sites as a whole, the other three species lag far behind F.lemani in site appropriation, and all at about the same level. As can be seen from Fig. 13 the overall picture for these three species was one of very gradual expansion, with M.rubra showing signs of fluctuation in number of sites colonised. Figure 13a suggests that the general expansion after the initial immigration phase is maintained at a steady rate for the next two years, and that the impetus then starts to slow up over the fourth and fifth years. It will be seen that this is due to the dominating effect of the F.lemani curve, and, to a lesser extent, that of M.rubra, M.scabrinodis and L.acervorum continuing to expand at about the same rate throughout. It should be noted that, even after four years, the quadrats are still unsaturated.

In the course of the investigations it soon became evident that there existed a certain amount of colony or territory instability in each species, that is an instabi[C] represents the number of co as distinct from number. A method was therefore formulated to express the relative instabilities of the various species being considered. It can be represented as follows:

$$I = \frac{V}{V + C} \times 100 \text{ percent.}$$

Where..... I is percentage instability over a given period

V represents the number of nest vacations during the period

C represents the number of continuances during the period.

The results are shown in Table 1.

Table 1.

Nest Instabilities over the Period 1952-1954

	F.lemani	M.scabrinodis	M.rubra	L.acervorum
Sandstone quadrat	8.3	0.0	----	50
Basalt quadrat	----	0.0	----	100
Slate quadrat	0.0	----	100	----
Triplet sandstone	10	0.0	33	100
Triplet basalt	17.7	0.0	20	100
Triplet slate	0.0	----	0.0	100
Total triplet	0.0	0.0	22.2	66
Total sandstone	8.8	0.0	33	66
Total basalt	17.7	0.0	20	100
Total slate	0.0	----	60	100
Large sandst. quad.	7.1	0.0	----	100

(---- no reckonable colonisation)

The figures for the quadrats (which were all unsaturated) present an approximation to natural conditions with relatively distinct nest sites. The effect of concentration into triplets, however, while bringing the question of instability into sharper focus, also exhibits certain apparent anomalies where the igneous units are concerned. These, however, are easily explained in terms of the more normal open quadrat instabilities. Considering F.lemani in the above table, the instability figure for triplet basalt is obviously a contagious one due to the proximity of slate. Where M.rubra is concerned, the avoidance of the slate units in the triplets by M.scabrinodis has apparently had a steadying influence, and M.rubra is

completely stable in the slate with an overspill to the other two rock-types. The picture is thus one of F.lemani and M.scabrinodis clinging to their preferred sites, with M.rubra closely confined to what is left.

The average instabilities for the whole experimental area were as follows:-

F.lemani	M.scabrinodis	M.rubra	L.acervorum
8.8	0.0	38	89

M.scabrinodis was completely stable in all conditions during the 1952-1954 observation series. It never colonised slate. F.lemani and M.rubra come next in order, and, lastly, L.acervorum which was highly unstable under all circumstances.

2.4.2 Effect of dilution of insolation surface:

As can be seen from Figs. 1 and 1a, the colonisation in the open sandstone quadrat followed much the same pattern as that in the more closely knit sandstone quadrat (Figs. 14 and 14a). A difference only becomes apparent when the latter part of the observation period (i.e. 1954-1956) is considered. In the open quadrat, which was 81% colonised in July 1954, F.lemani showed no expansion between then and September 1956. M.scabrinodis did, however, expand by one unit in this time. Over the same period L.acervorum, typically volatile, disappeared.

In the condensed quadrat, which was 76% colonised in July 1954, F.lemani continued to expand (although at a reduced rate), while M.scabrinodis - hold territory declined. By 1956, the non-colonised units (a buffering no man's land) which had

extended round the M.scabrinodis - held territory, had been overrun and the foothold of the latter species reduced from the 1954 total of five to a precarious single unit. L.acervorum expanded by two units - as a plesbiont in both cases. M.rubra was not recorded from either quadrat.

The situation may be conveniently illustrated by a comparison of the respective instabilities:-

	Condensed quadrat	Open quadrat	
F.lemani	7.1	8.3	1952-54
M.scabrinodis	0.0	0.0	
F.lemani	0.0	0.0	1954-56
M.scabrinodis	80	0.0	

The 1954-56 values are necessarily based on two readings, compared with five for the 1952-54 period as explained in the introduction.

The instability of F.lemani during the 1952-54 period, although of a low level in both cases, was apparently slightly reduced by the more compact insolation surface. M.scabrinodis was completely stable in both quadrats. Over the second two years, however, the position in the condensed quadrat was strongly reversed, and in the open quadrat also F.lemani was completely stable.

The explanation of the above apparent inconsistencies may lie in the polydomous tendencies of F.lemani population growth which became apparent in the course of the investigations. This species appears to be able to bridge the gaps between scattered insolation sites better than either of the myrmecines

(as might be expected, considering the faster rate of travel under conditions of incoming radiation, Page 32). This tendency, magnified by increasing population pressure, has succeeded in stabilising F.lemani, and, reinforced by the greater degree of intimacy in the condensed quadrat, has finally caused M.scabrinodis to withdraw. It appears that, of the three methods of nest territory capture described by Brian (1952a), viz.,

(a) Gradual encroachment in the nest,

(b) Occupation following greater site tenacity in adverse conditions,

(c) Seige, causing total evacuation,

the main one in operation here is the first, an inescapable corollary of F.lemani population growth in such a closely knit insolation system.

In the above paper, Brian also describes how the nest architecture of M.rubra typically differs from that of M.scabrinodis, the latter species building strongly mudded cellular systems while the nests of M.rubra are lightly constructed and less cellular. He also found that M.scabrinodis had greater site tenacity than M.rubra, and that it was more agressive than the latter species. The same author (1952b) described how M.scabrinodis can be excluded from the choicest sites by F.lemani and found that M.scabrinodis replaces M.rubra when the latter species may be dislodged by unfavourable climatic conditions. He mentions the experimental demonstration by Gosswald (1938,1941) that M.scabrinodis is more tolerant of, and resistant to, low humidities.

2.4.3 Distribution of the various species among the three different rock-types:

On examination of the

distribution curves (Figs. 15 to 19), it will be seen that for F.lemani and H.scabrinodis, sandstone is never ousted from first place by the other two rock-types. Slate comes second in the F.lemani distribution, but was not colonised at all by H.scabrinodis. The H.rubra and L.acervorum records, however, contrast markedly with those of the other two species, there being evidence of much fluctuation between rock-types. This might be expected, bearing in mind the relative instabilities already described.

On subjecting the whole range of observations to analysis (Page 24), it was found that the probabilities of the rock-type distribution being a random one were:

F.lemani	H.scabrinodis	H.rubra	L.acervorum
.01	.01	.85	.3

Thus F.lemani and H.scabrinodis are the only two species showing any steady "preference" (both for sandstone). This being the case, any comparison of interspecific rank or analysis of concordance would be worthless. This situation supports the indications already derived from the instability measurements that, in the normal open quadrats, H.rubra is relatively passive to F.lemani and H.scabrinodis. The possibility of the distribution of H.rubra being due solely to wider tolerances of microclimate is not supported by its high instability figure. L.acervorum, being a potential plesbiont, is not subjected to the same pressure as regards nest sites.

As an extension of this aspect of the colonisation picture, an investigation was carried out on the temperature characteristics of the air space under the different rock-types with a view to determining whether this might have any significant

eco-differentiating influence.

The method employed was as follows:

Nine rock units (three from each of the main quadrats) were chosen for the investigation, the choice being random within each rock-type. Ordinary glass-stem thermometers were employed, and in order to minimise the normal conductive risks inherent in their use were laid in troughs, 2 cms deep, cut in the turf, and with their bulbs projecting into the cavities below the rock units. The bulbs were enclosed in a non-absorbent cotton-wool film for protection. When the thermometers were in position, the turf strips were replaced over the stems and pressed down. A section of each strip was cut to facilitate removal for temperature readings with minimum disturbance of the temperature relations.

Typical daily temperature regime curves obtained are shown in Figure 20. From these curves it can be seen that the basalt units have more of a buffering effect on the temperature of the underlying air space, being cooler under incoming, and warmer under outgoing radiation conditions when compared to the other two rock-types. The latter react more quickly to changes in the radiation cycle, the sharp rise after dawn being especially well marked.

The greatest temperature difference recorded was at 8 a.m., when the warmest unit (a sandstone) was eight centigrade degrees warmer than the lowest basalt. At dawn, the highest basalt reading was four degrees warmer than that of the lowest sandstone, whereas at 2 p.m. the highest sandstone reading was five degrees warmer than that under the lowest basalt.

The greatest temperature fluctuation (twenty-six centigrade degrees) over the twenty-four hours was shown by a sandstone unit, and the least (seventeen centigrade degrees) by a basalt unit. The slate units show slightly more erratic temperature effects than the other two types, and are apparently more susceptible to the effects of slight differences of aspect in relation to the sun. This would be expected, taking into account their much smoother surface and higher reflectance over the visible range (Page 65).

The results obtained thus indicate a possible reason for the popularity of sandstone and slate units as compared with basalt, a lively response to incoming radiation and a high midday temperature being preferred to a more sluggish rise and a lower maximum. Should, however, the temperature in the space immediately under the stone rise to a dangerously high level, the brood can simply be moved to a deeper and cooler part of the nest.

2.5 Summary

(a) In order to investigate some aspects of nest appropriation and subsequent nest stability among moorland ant species, the insolation-trapping potential of a small area of *Agrostis/Festuca* plagioclimax was increased by placing stones on the surface of the grass.

(b) Three different rock-types (sandstone, basalt and slate) were used for these potential nest-sites in an attempt to detect any effect of the different thermal properties of the rock-types on subsequent colonisation.

(c) Resulting colonisation was recorded at intervals over the succeeding two years, and again after four years had elapsed.

(d) Formica lemani showed the greatest initiative and continued drive in colonisation of the new sites presented. The other three ant species were slower in appropriation of the new nest-sites, both Myrmica scabrinodis and Leptothorax acervorum showing a gradual increase in number of nests from year to year. Myrmica rubra, on the other hand, showed a decrease in nest number after two years, at the time when the overall colonisation figure reached a plateau. It would appear, therefore, that the decrease in M.rubra was due to the ever-increasing intimacy of contact with the other species.

(e) Although the potential nest-sites were not all occupied four years after laying, the main expansion took place in the first two years, there being little change thereafter.

(f) With regard to nest stability, as distinct from number, M.scabrinodis was the most stable of the four species considered during the first two years. Once it had colonised a nest-site it never vacated it. This was true for all the rock-types colonised except slate, which was never colonised by this species. F.lemani and M.rubra come next in order of nest stability, F.lemani being completely stable under all slate, and M.rubra being completely stable under the slate of the triplet units only. L.acervorum was highly unstable under all circumstances.

(g) An increase in the ratio of insolation surface to the area between the surfaces appears to favour F.lemani by enabling it to expand by gradual encroachment.

(h) F.lomani and H.scaberinodis were the only species showing any steady "preference" for a particular rock-type. This was sandstone in both cases. Slate came in second place for F.lomani, but this rock-type was never colonised by H.scaberinodis. H.rubra and L.acervorum showed much fluctuation with regard to rock-type.

(i) Basalt units had a greater smoothing effect on the daily temperature regime of the underlying airspace than either of the other two rock-types. Sandstone and slate units showed a lively response to incoming radiation and a higher midday temperature.

Tests of significance of the species distribution among the three rock-types .

(a) P.lennani :

	Total Recordings		
	Sandstone	Slate	Basalt
Observed:	64	51	54
Expected:	50	50	50
Difference :	14	1	16

$$\chi^2 = \frac{14^2}{50} + \frac{1}{50} + \frac{16^2}{50} = 9$$

d.f. = 2 P = .01

(b) H.seabrinodis:

	Total Recordings		
	Sandstone	Slate	Basalt
Observed:	18	0	9
Expected:	9	9	9
Difference:	9	9	0

$$\chi^2 = \frac{9^2}{9} + \frac{9^2}{9} = 18$$

d.f. = 2 P = <.01

(c) H.rubra :

	Total Recordings		
	Sandstone	Slate	Basalt
Observed:	7	6	8
Expected:	7	7	7
Difference :	0	1	1

$$\chi^2 = \frac{2}{7} = 0.285$$

d.f. = 2 P = 0.85

(d) L.neervoorn :

	Total Recordings		
	Sandstone	Slate	Basalt
Observed:	8	4	10
Expected:	7.3	7.3	7.3
Difference :	0.7	3.3	2.7

$$\chi^2 = \frac{0.7^2}{7.3} + \frac{3.3^2}{7.3} + \frac{2.7^2}{7.3} = 2.6$$

d.f. = 2 P = 0.5

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3. Foraging Activity

3.1 Introduction

Having considered the possible eco-differentiating significance of colonising drive, nest stability and the possible effect of different rock-types, attention was then turned to the question of foraging activity, and to the possibility of specific differences being present here also.

Emphasis was placed on an investigation of the above ground or extra-nest activity cycles of the three main ant species present in the experimental area, i.e. F.lemani, M.ruba and M. scabrinodis. The supplementary aspects of foraging range and speed of travel were also considered. It had already been shown by Brian (1955) that there was a difference in the tendency to climb during foraging, this tendency being most highly developed in F.lemani and least so in M.scabrinodis. M.ruba was intermediate in this respect.

3.2 Methods

These observations were carried out in the area already described. The selected nests were prepared for observation by cutting out a narrow but deep ring of turf and soil round them, down to bedrock where possible, and at a sufficient distance from the nest centre to ensure the minimum of damage to the main fabric

of the nest. Plaster of Paris was then poured into the excavation until level with the soil surface, thus isolating the nest by blockage of underground galleries, and forcing all ants entering or leaving the nest to use surface openings within the ring. The nests were prepared two days before observations were made, on each occasion. The ants quickly adapted themselves to this situation and were counted as they crossed the plaster. Push-button tally counters were used.

In all, thirty nest/day continuous observations were made (ten for each species). Six nests (two of each species) were used on any one day. Observations began at 5.00hrs and continued without interruption until 20.30hrs G.M.T. Activity at each nest-site was counted for fifteen minutes in each hour, the two nests of the same species being observed in adjacent periods. The activity of each nest was thus checked once every one and a half hours. Besides these whole-day observations, many supplementary counts were made over shorter periods. Nocturnal activity was checked on three occasions using both direct observation of ringed nests and pitfall trapping over a wider area. Separate counts were made of the ants entering and leaving the nest during each observational interval.

Humidity, air temperature and soil temperature readings were made halfway through each interval, the soil thermometer being inserted to a depth of three centimetres next to the stone covering the nest. The wet and dry bulbs were placed among the grass two centimetres above the soil surface and shielded from direct insolation (Plates 2, 3, 4, and 5).

3.3 Results

Given ideal weather conditions, i.e. little or no wind,

full sun and consequently regular temperature and humidity regimes, the activity curve of F.lemani is unimodal with a peak at about midday, while those of M.rubra and M.scabrinodis are bimodal, with peaks in the forenoon and afternoon separated by a low at midday. Figures 21, 22 and 23 are typical for the three species under these conditions. Fluctuations in temperature, due to cloud or showers, were reflected by less marked bi-modality of the myrmecine activity patterns and destruction of the single peak typical of Formica.

The activity maxima and midday minima for Myrmica and the maxima for Formica, which were recorded during the whole-day observations, are plotted against time and dry-bulb temperature in Figures 24, 25 and 26. Activity of Myrmica continued at a reduced intensity throughout the night, even in bad weather, whereas Formica typically did not leave the nest during the night.

3.4 Discussion

The results show that the activity cycles of M.rubra and M.scabrinodis differ markedly from that of F.lemani, the first two species showing a depression at midday while the latter species is most active at this time. This is thus a good example of integration and maximal utilisation of space-time (Park, 1941). Talbot (1946), working with North American species of Formica and Myrmica, obtained results similar to the above.

The activity curves of the myrmecines differed slightly from one another as well, the forenoon maximum of M.rubra typically occurring between 8.00hrs and 10.00hrs while that of M.scabrinodis occurred between 9.00hrs and 11.00hrs. This approximation of the M.scabrinodis activity peaks may

possibly be due to the lower level in the turf at which this species forages, and consequently shorter period of possible exposure to direct sunlight.

The question as to what factors govern these marked activity cycles is one of extreme interest, as is that of the mechanism responsible for the great difference in the periodicity curves of Myrmica and Formica.

M.ruba's peaks of activity came between 15°C and 20°C. No lower limit of activity was observed, however, foraging continuing on a reduced scale all night. The peaks of M.scabrinodis lay between 17°C and 22°C for the most part, and again foraging was seen to continue on a reduced scale all night.

F.lemani showed a maximum of activity between 21.5°C and 28°C, while the threshold for above-ground activity appeared to be between 10°C and 15°C. Due to the active transpiration from the turf, and the fact that the myrmecines typically foraged at a fairly low level, it is not considered that relative humidity played any significant part in influencing the various activity cycles described. Light and/or temperature appear to be the main controlling factors, with temperature playing the most important role in limiting myrmecine activity at midday (the minima for Myrmica occurred mainly between 12.00hrs and 15.00hrs when temperature is at a maximum), and light intensity controlling the time of F.lemani maxima (the peaks for this species being equally distributed about 12.00hrs, the time of maximum light intensity).

This raises the question of the possible significance of the differences in integumental colour, thickness and surface sculpturing which exist between F.lemani on the one hand and

the myrmecines on the other. In this connection, investigations were undertaken to compare the cuticles of Myrmica and Formica as regards thickness and transmissivity for both visible and infrared regions of the spectrum. The description of these measurements is given on Page65&67. Stating the results briefly, the Formica cuticle is melanic, thin and shagreened on the outer surface; the Myrmica cuticle is pale, about three times thicker than that of Formica, and shiny. The transmissivity of F.lemani cuticle was less than 10% that of Myrmica at the ultraviolet and of the visible spectrum, and rose fairly steadily to 60% of that of Myrmica in the near infrared (Fig.30). As regards transmissivity in the infrared proper, there was no great qualitative difference between the two cuticles, the absorption curves obtained (Figs. 31 & 32) resembling those obtained by Richards (1951) for Periplaneta and Thermia.

These results suggest, therefore, that under incoming radiation conditions the integument of Formica stops more short wavelength radiation than does that of Myrmica, and that this has the effect of (a) affording protection against the more harmful part of the spectrum

and (b) increasing the temperature of the integument and hence that of the body generally.

This is obviously an advantage to an insect with a normally high metabolic rate living in surroundings with a fairly low ambient temperature. Another aspect of the dark-coloured, thin and shagreened cuticle of Formica is that it would enable rapid elimination of excess body heat by re-radiating this to cooler surroundings when the ant is in the shade.

This would be an advantage should the body temperature rise above the optimum level due to intense insolation, since a short period spent in a shaded situation would enable relatively rapid loss of heat. This is, of course, a disadvantage when there is no incoming radiation, and the ambient temperature is low (i.e. at night).

In a recent review of periodicity of flight by insects, Lewis and Taylor (1965) discuss the question of colour in relation to day and night flight. They found that night-flying Nematocera were mostly pale in colour, and that they contrasted sharply with the day-fliers. These authors are of the opinion that the evolutionary trend in Nematocera may lead to their flying at night when wind speed is less and predators possibly fewer. They go on to say that although the temperature is lower at night, the absence of ultraviolet light, the slight gain in temperature due to loss of pigment and maintenance of this gain due to increased body size may be enough to make night flight possible. The above paper does not consider differences in cuticular thickness as a substitute for body size from the heat conservation aspect, however in the case of the ant cuticle being considered here the insulation provided by the thicker shiny myrmecine cuticle would appear to be of help in conserving body heat under low temperature conditions.

To sum up, the myrmecines appear to be adapted for conservation of body heat and are thus placed at a disadvantage when the ambient temperature is high. Formica, on the other hand, is adapted to conditions of high light intensity and is in consequence at a disadvantage at low ambient temperatures.

As a supplement to the above, foraging range and speed of the three main species were investigated by presenting foraging workers with Drosophila pupae (marked with aluminium dust) or cake crumbs, then timing their return to the nest and at the same time plotting their route by means of small metal tags. The total distance covered was then measured.
All measurements were made during the period of maximum activity for each particular species.
Results were as follows:-

Maximum Range

Species	Maximum range in metres	Av. speed in cm/min.
F.lemani	18	82
M.rubra	3.3	27
M.scabrinodis	3.0	10

Maximum Speed

Species	Range in metres	Av. speed in cm/min.
F.lemani	15	130
M.rubra	3.3	27
M.scabrinodis	1.2	15

Thus the shorter daily period which F.lemani spends in foraging is compensated for by greater range and speed.

It may conveniently be noted here that the shape of the base of the antenna differs markedly between M.rubra and M.scabrinodis. The latter has a much sharper bend at the base which enables the antennae to be laid back more closely to the head when the ant is moving in a confined space. This would

thus facilitate foraging at a lower level than M.rubra as has been shown by Brian (1955) when investigating foraging stratification in F.lemani, M.rubra and M.scabrinodis. The latter author found, by means of trapping experiments, that M.scabrinodis foraged principally on the soil surface, and perhaps below. F.lemani readily climbed vegetation, while M.rubra was intermediate in this respect.

3.5 Summary

(a) Extra-nest activity cycles of F.lemani, M.rubra and M.scabrinodis were investigated by means of isolating nests in plaster rings and counting foragers as they crossed the plaster.

(b) Formica was found to have quite a different activity pattern than both Myrmica species. Under ideal weather conditions the former shows a unimodal activity cycle with the peak at midday, whereas the cycles of M.rubra and M.scabrinodis are bimodal with peaks in the forenoon and afternoon.

(c) The activity maxima of Formica are grouped around noon, the time of maximum intensity of insolation, whereas the minima of Myrmica appear to be affected rather by the time of maximum air temperature in early afternoon.

(d) Both Myrmica species continued to forage on a reduced scale during the night. Formica did not forage at night.

(e) F.lemani foragers were found to travel faster and farther than either of the Myrmica species, the shorter daily period

which F.lomani spends in foraging thus being compensated for by greater range and speed.

(f) These differences may be explained in terms of the differences in the integuments of Formica and Myrmica in regard to thickness, colour and surface texture. The myrmecinae appear to be adapted for conservation of body heat and are thus placed at a disadvantage when the ambient temperature is high. Formica, on the other hand, is adapted to conditions of high light intensity, and is in consequence at a disadvantage at low ambient temperatures.

(g) The antennal base of M.scabrinodis is sharply bent, facilitating foraging lower down in the turf than either of the other two species.

4. The Ant-Aphid-Plant Relationship

4.1 Introduction

As part of the investigation of possible eco-differentiating factors effecting ant species in the West of Scotland, a survey was made of the plants of the area which most commonly act as hosts to myrmecophilous aphids, and which are thus utilised by ant colonies to which they are a major source of carbohydrate and also a source of protein (Schmidt, 1952). The nutritional importance of honeydew for various insects has been investigated by a good number of authors.

As a result if investigations of the effect of a Pseudococcus citri Risso honeydew diet on the reproduction of certain species of fruit-flies, and also the effect of synthetic foods on Chrysopa californica Coquillett which has P.citri honeydew as a natural diet, Hagen (1950, and personal communication) has shown that this particular honeydew, at least, contains essential nutrients required for effective fecundity and fertility, viz.,carbohydrates,hydrolysed protein,minerals,B vitamins and a male fertility factor. The exploitation of sources of honeydew by Apis mellifica Linn., has been shown, and Nixon (1951) describes its utilisation by beetles and butterflies. Gray (1952) found 16 free amino acids and several carbohydrates (including fructose,

glucose and sucrose) in the honeydew of the Pineapple Mealybug Pseudococcus brevipes Ckl. He also found five amino acids in the honeydew which were not found in the food-source of the mealybug. Free amino acids were found also in the honeydew excreted by the crescent-marked Lily Aphid, Hyperomyzus circumflexus Buck., by Maltais and Auclair (1952). They found 22 free amino acids and amides, including all the essential amino acids known to be required by animals for growth. The amino acids constituted 13.2% of the excretion, as against 35.7% of invert sugar. Swart (1956) found that the amino acids produced by five different coccid species were the same.

Apart from physical damage to the plant, caused by abstraction of sap and direct tissue destruction, the aphids and coccids act as vectors of various pathogenic organisms, viral, fungal and bacterial, and, where not closely attended by ants, may provide the initial medium in the form of honeydew for the growth of sooty moulds (Carter 1933a, 1933b, 1955, 1942; Serrano 1934).

The term "myrmecophilous" is broad in scope, and may be somewhat misleading (Janet 1897), including as it does so many different types and grades of association, and also implying that the ants are actually sought out by the myrmecophile. Wasmann's term "trophobiosis", described by Wheeler (1928), covering the particular type of association involving aphids and coccids, is much more descriptive and useful. The relations existing between aphids and ants seem to vary widely from intimate symbiosis to mere adventitious association, and while some of the aphid species listed below may not be accepted as

obligatory trophobionts, they are at least tolerated and thus afforded passive protection. It is emphasised that this account deals solely with aphids found in the nest or adjacent galleries, and that more casual extra-nest association, which are of little importance in this region in any case, are not considered.

4.2 Method

Aphid and plant samples from ants' nests were taken from various localities between Dumbarton and Glen Falloch. Equipment consisted of a trowel, sheath knife and fine forceps for excavation of the nest, with glass tubes and tins to contain aphid and plant specimens. All aphid samples, and most grasses, were identified in the laboratory, the aphids being preserved in the field in lactic alcohol. There was no emphasis placed on any particular ant species, thus the number of records for each ant and myrmecophile species is a broad indication of its relative abundance in the area. The islands in Loch Lomond were not included in the survey.

Leptothorax acervorum F., occurred frequently in the course of the investigation, but mainly as a plesbiont. In the few cases where isolated Leptothorax nests were investigated no aphids were found. As regards the other ant species, no aphids were evident in the nest itself in many cases at first, but during the examination, which often involved the destruction of the fabric of the nest, they were usually discovered in one of the galleries, sometimes at a considerable distance from the nest centre. The number of nests which yielded no aphids formed about 12% of the total examined.

4.3 Results

The results of the survey are set out in Tables 2 to 7.

In the majority of cases (Table 3) the nests contained one aphid species on one food plant. In six cases the single species of aphid was spread over two food plants (Table 4). Twenty-two nests each contained two aphid species, and in two of these each species was feeding on a different plant species (Tables 5 and 6). The maximum number of aphid species found in the same nest was three, which occurred four times (Table 7). In each of these four instances the three insect species were feeding on the same food plant.

It will be seen from Table 2 that the Gramineae suffer most as hosts of the trophobionts, especially Agrostis alba and A.tenuis, with Festuca rubra in third place. Lower in the scale, and all about the same level, come Aira flexuosa, Festuca ovina, Holcus mollis and Poa pratensis. The commonest triple association found was: Formica lemani, Forda formicaria and Agrostis alba, but it will be seen that the range in association is a wide one, and that a great degree of adaptability is evident in these relationships.

Forda formicaria was by far the most frequently occurring aphid, and the most polyphagous, with Tetraneura ulmi and Anoecia corni also prominent. Where, however, the vegetation type is completely unsuitable, even for these polyphagous and highly adaptable species, other species are usually available to take up the role of adventitious trophobiont. A striking example of this was noted by the writer on the Isle of Mull, where large thriving colonies of Lasius niger (an ant rare in Dunbartonshire) were found associated with Aphis newtoni Theobald for which the ants had constructed earthen shelters round the bases of the leaves of Iris pseudacorus L.

Table 2.

The Species Recorded and their Frequency

APHIS

Ingius flavus Fab.	62
I.niger L.	3
Formica lemani Bondroit	719
Myrmica rubra L.	65
M.scabrinodis Nylander	33
M.laticornis Nylander	1

APHIDS

Anoecia corni Fab.	48
A.vagans (Koch)	1
Aphis cracciverm (Koch)	2
A.confusa Wlk.	1
A.scorodoniae Del Gu.	2
A.tormentillae Pass.	1
Baizaurea pistaciae L.	1
Forda formicaria Heyden	154
Geoica pellucida (Buckton)	6
G.setulosa (Pass.)	2
Jacksonia papillata Thoob.	1
Rhopalosiphum insertum (Wlk.)	2
Siphs glyceriae (Kalt.)	5
Tetraneura ulmi (L.) Halliday	87

Table 2 (Continued)

PLANTS

Agropyron repens Beauv.	1
Agrostis alba L.	86
A.canina L.	2
A.tenuis Sibth.	68
Aira caryophyllea L.	2
A.flexuosa L.	15
Alopecurus pratensis L.	4
Cynosurus cristatus L.	1
Festuca ovina L.	15
F.rubra L.	50
Holcus lanatus L.	2
H.mollis L.	13
Hollnia caerulea Moench.	3
Poa pratensis L.	12
Juncus articulatus L.	3
Luzula campestris L.	4
Potentilla erecta (L.) Rausch	1
Rumex acetosella L.	3
Succisa pratensis Moench.	1
Teucrium scorodonia L.	2
Trifolium spp.	3

Table 3. Nests Containing a Single Aphid Species on One Plant Species (Figures in this and the following tables show the number of times each association was recorded)

HOST PLANTS

ANTS	APHIDS	Agropyron repens	Agrostis alba	A.canina	A.tenuis	Aira caryophyllea	A.flexuosa	Alopecurus pratensis	Cynosurus cristatus	Festuca ovina	F.rubra	Holcus lanatus	H.mollis	Molinea coerulea	Poa pratensis	Juncus articulatus	Luzula campestris	Potentilla erecta	Rumex acetosella	Succisa pratensis	Teucrium scorodonia	Trifolium spp.
	Anoecia corni	-	2	-	7	-	-	-	-	2	3	-	-	-	-	-	-	-	-	-	-	-
	A.vagans	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
	Forda formicaria	-	10	-	2	2	-	-	-	-	3	-	-	-	1	-	-	-	-	-	-	-
Lasius	Aphis scorodoniae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
flavus	Geoica setulosa	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	G.pellucida	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Baizongia pistaciae	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Tetraneura ulmi	-	2	-	3	-	2	-	-	1	3	-	-	-	1	-	-	-	-	-	-	-
Lasius	Anoecia corni	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
niger	Tetraneura ulmi	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Anoecia corni	-	1	-	4	-	-	1	-	-	4	-	1	-	-	-	-	-	-	-	-	-
	Forda formicaria	-	22	1	12	-	3	1	-	8	8	-	2	-	10	-	1	-	1	-	-	-
Formica	Aphis craccivora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
lemani	A.tormentillae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
	A.scorodoniae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
	Tetraneura ulmi	1	5	-	2	-	7	-	-	2	7	-	1	-	-	-	-	-	-	-	-	-
Myrmica lobicornis	Forda formicaria	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Anoecia corni	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Forda formicaria	-	6	-	5	-	2	1	1	-	7	-	1	-	-	-	2	-	1	-	-	-
	Aphis craccivora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Myrmica	Jacksonia papillata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
rubra	Rhopalosiphum insertum	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Sipha glyceriae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
	Tetraneura ulmi	-	7	1	4	-	-	1	-	-	1	-	5	-	-	-	-	-	-	-	-	-
	Anoecia corni	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myrmica	Forda formicaria	-	3	-	8	-	-	-	-	1	3	-	-	2	-	-	-	-	-	-	-	-
scabrinodis	Aphis confusa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
	Sipha glyceriae	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Tetraneura ulmi	-	5	-	3	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-

Table 4. Nests Containing a Single Aphid Species on Two Plant Species

ANTS	HOST PLANTS: Agrostis alba	Alopecurus pratensis	Festuca rubra	Holcus mollis	Luzula campestris	Rumex acetosella	APHIDS
Formica lemani	1	-	1	-	-	-	Forda formicaria
F.lemani	1	-	1	-	-	-	F.formicaria
F. lemani	1	-	-	-	-	1	F.formicaria
Myrmica rubra	-	1	-	1	-	-	Tetraneura ulmi
M.rubra	1	-	-	-	1	-	F.formicaria
Lasius flavus	1	-	1	-	-	-	Geoica pallucida

Table 5. Nests Containing Two Aphid Species on One Plant Species

ANTS	HOST PLANTS	APHID: Forda formicaria	Geoica utricularia	Anoecia corni	Rhopalosiphum insertum	Sipha glyceriae	Geoica pellucida
	Alra flexuosa	1	1	-	-	-	-
	Agrostis tenuis	1	-	1	-	-	-
	Festuca rubra	1	1	-	-	-	-
Formica lemani	F.rubra	-	1	1	-	-	-
	F.rubra	1	1	-	-	-	-
	F.ovina	1	1	-	-	-	-
	Holcus mollis	1	-	1	-	-	-
	Agrostis alba	1	-	-	1	-	-
	A.tenuis	1	-	1	-	-	-
Myrmica rubra	A.tenuis	1	1	-	-	-	-
	Festuca rubra	1	1	-	-	-	?
	Holcus mollis	1	1	-	-	-	1
M.scabrinodis	Agrostis alba	-	1	-	-	1	-
	A.tenuis	-	1	1	-	-	-
	A.tenuis	1	1	-	-	-	-
Lasius flavus	A.tenuis	-	1	1	-	-	-
	A.alba	1	-	-	-	-	1
	Festuca rubra	1	1	-	-	-	-
	F.rubra	1	-	1	-	-	-
L.niger	A.alba	-	1	1	-	-	-

Table 6. Nests Containing Two Aphid Species on Two Plant Species (each on a different plant species).

ANTS	APHIDS	HOST PLANTS
Myrmica rubra	Tetraneura ulmi	Agrostis alba
	Sipha glyceriae	Juncus articulatus
M.scabrinodis	Forda formicaria	Molinea coerulea
	Anoecia corni	Agrostis tenuis

Table 7. Nests Containing Three Aphid Species on One Plant Species

	APHIDS				
ANTS	Forda formicaria	Tetraneura ulmi	Anoecia corni	Cerica pellucida	HOST PLANTS
Formica lemani	1	1	1	-	Festuca rubra
Lasius flavus	1	1	-	1	Agrostis alba
L.flavus	1	1	1	-	A.alba
L.flavus	1	1	1	-	A.tenuis

Aphids were most numerous and obvious in the nests in spring and autumn. In early summer Formica lemani and Myrmica rubra have been observed removing Forda individuals from the nest and releasing them in the open. Both Forda and Tetraneura have been seen wandering on the turf surface during the summer, free from any regimentation. Adult viviparae of these two species appear on the grass rhizomes near the surface layers of the nests in early spring, then the population builds up rapidly. While Forda and Tetraneura thus appear to overwinter as viviparous females deep in the ant galleries, Anoecia does so in the egg. Eggs of Anoecia are collected, by Lasius flavus at least, and in spring are placed in small piles in insolation sites. They hatch in mid-April. In North America, however, Anoecia corni is said to overwinter in the adult state (Cutright 1925).

The nectaries of Potentilla erecta are also very attractive to ants as a source of sugar. Myrmica rubra, M.scabrinodis and Formica lemani workers have been seen frequenting these flowers and occasionally gripping the base of the styles and pulling, as though attempting to carry the sugar source back to the nest. Seeds of Potentilla erecta and Luzula sumestris are carried back into the nest, however, the latter being carried by the convenient basal appendage, but no evidence is available to show that these are used as food.

The only predators seen attacking aphids in the nests were syrphid larvae. Many of the aphid species listed also occur as pests of wheat and other cereals (Davidson 1925). The coccids Orthezia cataphracta Shaw and Ripersia spp., were also found in association with ants in the area covered, but

the importance of these in the food economy of ant colonies is probably realised, in this district, only in Callunetum.

4.4 Discussion

F.lemani, H.rubra and H.scabrinodis (being the species with which we are mainly concerned), the seven common plants and the three common aphids are considered specially. On ranking the "choices" of the ants for grasses and for aphids, and the "choices" of the aphids for grasses, then applying tests of concordance (Page 50), it is found that there is a high degree of concordance in all three cases. Further, on comparison of the ant and aphid ranking of grasses (Table 8) it is seen that there is close agreement.

Table 8.

Ant and Aphid Ranking of Grasses

Grass	Ant ranking	Aphid ranking
Agrostis alba	1.5	1
A.tenuis	1.5	2
Aira flexuosa	5	5.5
Festuca ovina	4	5.5
F.rubra	3	3
Holcus mollis	6	4
Poa pratensis	7	7

Bearing in mind the polyphagous nature of the aphids dealt with, it is difficult to accept the hypothesis that three ant species and three aphid species may discriminate identically between seven plant species. The associations between ant and plant, and aphid and plant, would therefore appear to be determined by

the composition of the sward. As regards the ant-aphid association, on the other hand, the concordance shown is again consistent with a random hypothesis dependent merely on aphid population density, but since these aphids occur only in association with ants there must be some explanation of the different population strengths. These are most probably due to one or more extraneous ecological factors, such as minute differences in microclimate, as any active preference on the part of the host would lead to drastic reduction in number of the less popular myrmecophiles.

In general there appears to be little specificity in the relations between Homoptera and the ants attending them. Strickland (1947) has shown that the cacao mealybug Pseudococcus nilgalensis Laing is attended by fifty species of ants. Jones (1929), working in Colorado, found that Formica fusca var. neoclara Emery attended forty-two species of aphids representing five genera, and F. fusca var. arrenten Wheeler thirty-one species representing fourteen genera (Bixon 1951).

Notwithstanding this apparent broad plasticity of ant-aphid association, Way (1953, 1954a, 1954b) has demonstarted the high degree of interdependence which may be evolved in one of these relationships. In the insects which he studied, Cecophylla longinoda (Latr.) and the coccid Saissetia zanzibarensis Williams, he found that the coccid and other honeydew-producing Homoptera were the principal food source of the ant. Deprived of these, Cecophylla longinoda can exist only at relatively low population levels. Conversely, the size of the Saissetia zanzibarensis population is dependent on the level of the ant population, excess coccids, both nymph and adult, being attacked and killed. Although the host plants suffered obvious feeding

damage under confined experimental conditions, this was not observed in the field as Oecophylla longinoda farmed out the coccid nymphs and maintained clusters on the host-plant twigs at a non-injurious level.

El-Sisdy and Kennedy (1956) have found a similar relationship between Lasius niger and Aphis fabae Scopoli as regards the aphid population level, but there is no active farming in this case, the aphids being allowed to wander freely. While the latter authors did observe a certain amount of active protection of the aphids by Lasius niger, they incline to the view that any benefits thus derived are mainly secondary in importance to the possibility suggested by Hersig (1937) that in ant-attended aphid colonies the increased growth is a result of the greater intake of food due to stimulation of secretion. Kennedy and Mittler (1953), however, have shown that the rate of flow of phloem sap through the severed mouthparts is very similar to the rate of excretion of honeydew by the intact insect, suggesting that in fact the aphid exercises little control on the flow of sap through its body, this being dependent mainly on the turgor pressure of the plant.

4.5 Summary

(a) A survey was carried out of the aphids and their host plants which were associated with ant colonies.

(b) Six ant species, fourteen aphid species and twenty-one plant species were recorded. Of these, four ant species, three aphid species and seven plant species occurred much more frequently than the others.

(c) Grasses were the main plants which were exploited, the species utilised being determined mainly by availability corresponding to sward composition.

(d) No specificity was found in the relationships between the common trophobiont myrmecophiles, the ants attending them and the host plants, and so the ant-aphid-plant relationship plays no obvious part in the eco-differentiation of the ant species considered.

Analysis of concordance of "choice" of R.fabae, R.rubus and R.crataegella for the three common aphids and the seven common plants, also the "choice" of the three common aphids for the seven common plants.

(a). The "choice" of R.fabae, R.rubus and R.crataegella for the three common aphids (considering the seven common plants only):-

	R.fabae (1)	R.fabae (11)	R.rubus (1)	R.rubus (11)	R.crataegella (1)	R.crataegella (11)	Rank Totals Actual	Rank Totals Expected
M.fabae-persicae	25	1	27	1	15	1	3	6
S.avenae	30	2	22	2	9	2	6	6
A.pisum	14	3	9	3	3	3	9	6

(1)....number of times the particular association was recorded.

(11)... ranking of the particular aphid in ant's "choice".

$S = 3^2 + 0 + 3^2 = 18$

$S_{max} = \frac{n^2(n^3 - n)}{12} = \frac{3^2(3^3 - 3)}{12} = 18$ $(n = 3;\ m = 3)$

Therefore the Coefficient of Concordance $(W) = \frac{S}{S_{max}} = \frac{18}{18} = 1$

W with continuity correction $= \frac{18 - \frac{1}{2}}{18 - \frac{1}{2}} = \frac{17.5}{20} = .85$

Friedman's $\chi^2 = \frac{(n-1)W}{1-W} = \frac{2 \times .85}{1 - .85} = 11.3$

Greater estimate degrees of freedom $= (n - 1) - \frac{2}{n} = 1.33$

Lesser estimate degrees of freedom $= (n - 1)\left[(n - 1) - \frac{2}{n}\right]$

$= 2.66$

Entering the tables for F with these degrees of freedom:-

10% level of F = 6.5

5% level of F = 13

1% level of F = 55.6

Therefore the complete concordance shown by the three ant species in their "choice" of aphids has a fairly low probability of occurring purely by chance (P is about .07).

(b) The "choice" of F.lemani, M.rubra and M.scabrinodis for the seven common grasses (considering the three common aphids only):-

	F.lemani (i)	F.lemani (ii)	M.rubra (i)	M.rubra (ii)	M.scabrinodis (i)	M.scabrinodis (ii)	Rank Totals Actual	Rank Totals Expected
A.alba	31	1	16	2	10	2	5	12
A.tenuis	19	3	19	1	13	1	5	12
A.flexuosa	11	4.5	2	5	0	6	15.5	12
F.ovina	11	4.5	0	6.5	1	4	15	12
F.rubra	25	2	9	3	3	3	8	12
H.mollis	5	7	8	4	0	6	17	12
P.pratensis	10	6	0	6.5	0	6	18.5	12

(i)....number of times the particular association was recorded.

(ii)....ranking of the particular grass in ant's "choice".

(Contd....

$$S = 7^2 + 7^2 + 3.5^2 + 3^2 + 4^2 + 5^2 + 6.5^2$$

$$= 202.5$$

$$S_{max} = \frac{m^2(n^3 - n)}{12} = \frac{3^2(7^3 - 7)}{12} \qquad (m = 3;\ n = 7)$$

$$= 252$$

Therefore the coefficient of Concordance (W) $= \frac{S}{S_{max}} = \frac{202.5}{252} = .8$

W with continuity correction $= \frac{202.5 - 1}{252 + 2} = .79$

Snedecor's F $= \frac{(m - 1)W}{1 - W} = \frac{2 \times .79}{1 - .79} = 7.5$

Greater estimate degrees of freedom $= (n - 1) - \frac{2}{m} = 5.33$

Lesser estimate degrees of freedom $= (m - 1)\left[(n - 1) - \frac{2}{m}\right]$

$= 10.66$

Entering the tables for F with these degrees of freedom :-

10% level of F = 2.5

5% level of F = 3.3

1% level of F = 5.4

Therefore the concordance shown by the three ant species in their "choice" of spittle grasses has a very low probability of occurring purely by chance (P is less than .01).

(c) The "choice" of F. fuscicornis, F.ulkei and A.cerni for the seven common grasses (considering the associations with F.lasani, H.rubra and H.scabrinodis only):-

	F.formicaria (i)	F.formicaria (ii)	F.ulmi (i)	F.ulmi (ii)	A.comm (i)	A.comm (ii)	Rank Totals Actual	Rank Totals Expected
A.alba	37	1	19	1	2	3.5	5.5	12
A.tenuis	28	2	10	3	16	1	6	12
A.flexuosa	6	6	8	4.5	0	6	16.5	12
F.ovina	10	4.5	3	6	0	6	16.5	12
F.rubra	24	3	15	2	6	2	7	12
H.mollis	5	7	8	4.5	2	3.5	15	12
P.pratensis	10	4.5	0	7	0	6	17.5	12

(i)....number of times the particular association was recorded.

(ii)...ranking of the particular grass in aphid's "choice".

$S = 6.5^2 + 6^2 + 4.5^2 + 4.5^2 + 5^2 + 3^2 + 5.5^2 = 183$

$S_{max} = \frac{m^2(n^3 - n)}{12} = \frac{3^2(7^3 - 7)}{12}$ $(m = 3;\ n = 7)$

$= 252$

Therefore the Coefficient of Concordance $(W) = \frac{S}{S_{max}} = \frac{183}{252} = .73$

W with continuity correction $= \frac{183 - 1}{252 + 2} = .72$

Snedecor's $F = \frac{(m - 1)W}{1 - W} = \frac{2 \times .72}{1 - .72} = 5.1$

Greater estimate degrees of freedom $= (n - 1) - \frac{2}{m} = 5.33$

Lesser estimate degrees of freedom $= (m - 1)\left[(n - 1) - \frac{2}{m}\right]$

$= 10.66$

Entering the tables for F with these degrees of freedom:-

10% level of F = 2.5

5% level of F = 3.3

1% level of F = 5.4

Therefore the concordance shown by the three aphid species in their "choice" of grasses has a low probability of occurring purely by chance (P is about .01).

5. Parasitism by Cysticercoids

5.1 Introduction

During dissection of ants collected from heather moor in Dunbartonshire in connection with nest "bagging" trials, two of the commonest species in this region, Myrmica rubra L. and M.scabrinodis Nylander were found to be acting as the intermediate hosts of a cestode. The cestode larval forms, the cysticercoids, lay freely in the body cavity of the ants, and were extruded as soon as the integument was ruptured.

5.2 Description of cysticercoids

The cysticercoids were ellipsoidal in shape (Fig.27), measuring 500-700μ by 340-400μ, were very active and contained numerous light-coloured granules. No suggestion of a cercomere was seen. The larval scolex was often extruded very soon after a cysticercoid was removed from an ant and placed in saline. In most cases the scolex broke away from the cyst, the rupture occurring at the base of the larval neck, and thereafter it progressed by movements of the suckers.

5.3 Description of larval scolex

The dimensions of the scolices varied with their state of contraction, but in their relaxed condition they were approximately 300μ long by 180μ in diameter. The rostellar ring was 50-60μ in diameter, and consisted of a double row of T-shaped hooks pointing outwards (Fig. 28). These hooks were 13-16μ in length and numbered about 180. The hooks of one row alternated with those of the other. The rostellum was invaginated in the scolex. The four suckers, 50-65μ in diameter, were each armed with one compact row of hammer-shaped hooks 8-12μ in length (Fig. 29). There were about 240 hooks per sucker, all pointing towards the centre.

5.4 Mode of occurrence

The cysticercoids were found in males, queens and workers of both the above Pyramica species, and it was soon discovered that the infected ants could be detected by an unnaturally dark chocolate coloration affecting the entire cuticle, compared with the dark reddish-brown tint of non-infected individuals. This colour difference may be due to the formation of a melanoid pigment from the excretions of the parasite, and appears to be distinct from the normal darkening of the cuticle due to age (J.S.Weir, personal communication).

Dissection of a large number (over one thousand individuals) of Formica lemani Bondroit and Leptothorax acervorum F. from areas in which Pyramica carried the infection failed to produce any cysticercoids (even though the L.acervorum samples were, on four occasions, phoresionts in infected Pyramica nests). These species were the only ones, besides M.rubra and M.scabrinodis which were of numerical importance in the area.

5.5 The definitive host

When the cysticercoids were discovered, a search was begun for the definitive host, or hosts, of the parasite. It was realised that the host need not necessarily be insectivorous, since oribatid mites had been demonstrated to be intermediate hosts of sheep cestodes (Stunkard,1939), and Krull and Mapes (1953) had shown Formica fusca L. to be a second intermediate host of the lancet-fluke Dicrocoelium dendriticum (Rudolphi) despite Cameron's (1931) demonstration of direct infection of sheep due to their swallowing infected snails.

The investigation was begun by examining the infected area for faecal material since this could be the only source of cysticercoid infection. The area consisted of the typical Agrostis/Festuca plagioclimax surrounded by heather. It was found that the droppings of the red grouse, Lagopus lagopus scoticus (Latham), were the most numerous, although traces of sheep and hare were also present. The droppings were carefully examined, and it was found that many of the specimens from grouse contained tapeworm proglottids. Twenty grouse intestines were obtained from birds shot in the area, and on examination all were found to be carrying heavy burdens of the widespread grouse cestode Raillietina (Fuhrmannella) tetragona (Molin). These occurred mainly in the small intestine, and one bird contained over forty tapeworms.

The scolices of a number of the adult worms from grouse intestines were removed, fixed and lightly stained. They were then dissected (using micro-manipulators) and the rostellar rings and suckers separated for examination, both in an intact condition and after maceration to separate the hooks. The larval scolices from the ant cysticercoids were similarly treated.

On examination, it was found that the larval and adult scolices were identical in all respects, the rostellar and sucker hooks being the same in number, size-range and shape in both cases.

As additional proof of the identity of the ant cysticercoid and the adult worm in the grouse, attempts were made to infect both grouse chicks and domestic fowl chicks by feeding them cysticercoids. Grouse eggs were obtained from a Perthshire moor and transferred to an incubator by a "Thermos" carrier. On hatching, the chicks were removed to an artificial brooder. Four were fed cysticercoids (in saline and in abdomens of infected ants), and two were kept as controls. Unfortunately the chicks were extremely difficult to rear and they all died within ten days after hatching. Examination of the intestines yielded no sign of incipient infestation, although a binocular microscope was used. The attempt to infect fowl chicks was also unsuccessful, although they survived until the experiment had to be terminated.

The feeding of Raillietina eggs to Formica (by mixing them in a sugar solution, and also by introducing ripe proglottids into laboratory nests) similarly produced no results.
It should be mentioned also that both F.rubra and F.sanguinea (but not F.lemani) foragers had been seen to carry off ripe proglottids (or bits of them) from grouse droppings during field observations. In this connection it is of interest to note that in the case of Anoplocephaline cestodes described by Stunkard (1939) it was only after a period of 2-5 months that the hexacanth larvae ingested by oribatid mites assumed a cysticercoid form capable of infecting sheep.

5.6 Occurrence and degree of ant infection

Further examinations of ants were carried out, samples being taken from both grouse-moor and lowland areas free from grouse. Cysticercoids were found only in ants from the former. Estimates based on dissection of over five hundred individuals of *F.rubra* and *F.sanguinea* from regions where the infection was detected, suggested that about eight percent were infected. Kates and Runkel (1948), found an infection of cysticercoids in oribatid mites to rise as high as thirty-four percent, but regarded four percent as a normal value.

Although the majority of infections consisted of a single cysticercoid, the number may be very much greater. The maximum observed was fifty from one *F.rubra* queen. A wide survey of distribution was not carried out, but infected ants were found in Perthshire as well as in Dunbartonshire.

5.7 Discussion

This parasite of the red grouse is a well known one, and received a great deal of attention in the final report of the Committee of Enquiry on Grouse Disease (1911). A number of investigators (A.E.Shipley, P.H.Grimshaw, W.Dygrave and others) attempted to discover the intermediate host of the tapeworm and examined different moorland insect groups, but did not find any cysts. Although adult red grouse are herbivorous (being mainly confined to a diet of *Calluna vulgaris* L.), the chicks are insectivorous, especially during the first fortnight after hatching (Committee of Enquiry on Grouse Disease, loc.cit.), and it therefore seems to be during this period that the massive cestode infections are picked up.

This appears to be the first recorded instance of the above two species of ant acting as the intermediate hosts of a cestode. H.F.Jones and H.W.Horsfall (1936) in the United States, have given an account of Tetramorium caespitum L. as an intermediate host of R.(Raillietina) echinobothrida (Megnin, 1881), and Ch. Joyeux and J.-G.Baer (1936, 1937) in France mention Tetramorium semilaeve Andre, also Pheidole sp. as transmitting the same worm. The latter authors further incriminate T.caespitum and Pheidole sp. as intermediate hosts of R.(Raillietina)tetragona (Molin, 1858), and Formica rufa L. as intermediate host of R.(Raillietina) friedbergeri (v.Linstow, 1878).

The class Cestoda includes three orders,Proteocephala, Cyclophyllidea and Pseudophyllidea, that have obligatory or facultative associations with arthropods. The family Davaineidae of the order Cyclophyllidea is composed of about twelve genera usually parasitic in the definitive form in birds. Of these, Raillietina species live as larvae in insects, and have been described from Carabidae and housefiies as well as from ants. Some members of this genus have been found in man (Horsfall,1962).

The differential parasitism,by the cestode described above, of Myrmica on the one hand and Formica on the other, is an indication of differences in food foraged and/or susceptibility to infection, and provides yet another factor to be considered in the eco-differentiation of the species as it would seem to place an added drain on the resources of Myrmica colonies inhabiting grouse-moor. An investigation of the possible effects of this parasitism on the reproductive potential of Myrmica would be of great interest.

5.8 Summary

(a) Males, queens and workers of *M.rubra* and *M.scabrinodis* from the experimental area were found to be harbouring infections of cysticercoids, which lay free in the body cavity.

(b) *F.lonnd* and *L.acervorum* were not parasitised by these larval cestodes.

(c) Infected specimens were distinguished by an unnaturally dark chocolate coloration affecting the entire cuticle.

(d) The majority of infections consisted of a single cysticercoid, but as many as fifty cysticercoids were obtained from one *M.rubra* queen.

(e) A comparison of *Myrmica* from moorland and lowland areas showed that only specimens from the former habitat were infected.

(f) The parasitism of *Myrmica* by these cysticercoids appears to be widespread on Scottish moors.

(g) The definitive host of the cestode was found to be the red grouse, *Lagopus lagopus scoticus* (Lath.), and the cestode itself was identified as *Ralliietina (Paroniella) urogalli* (Modeer), a member of the Davaineidae and a widespread parasite of red grouse.

(h) This differential parasitism of *Myrmica* and *Formica* may be considered as acting adversely on *Myrmica* in its colonisation of grouse-moor.

6. A comparison of certain characteristics of the cuticles of Myrmica and Formica and their possible significance in eco-differentiation.

6.1 Introduction.

As a further aspect in the consideration of possible eco-differentiating factors operating on certain moorland ant species, some attention was paid to the more outstanding differences of the cuticles of *Formica* and *Myrmica*, namely their thickness and colour, and to various implications of these.

6.2 Thickness.

Four specimens each of *Formica lemani*, *Myrmica rubra* and *Myrmica sculptinodis* workers were mounted in castor-wax blocks, one to a block, and trimmed on a microtome until a sagittal section was obtained. Measurements of cuticular thickness were then carried out on an ordinary microscope by reflected light using a spotlight and eyepiece micrometer. Mean values, to the nearest micron, were:-

		F.lemani	*M.rubra*	*M.sculptinodis*
Head	dorsal	9	23	26
	ventral	8	21	20

Contd..

		F.lemani	M.rubra	M.scabrinodis
Thorax	dorsal anterior	11	45	45
	dorsal posterior	8	25	18
	ventral	7	19	24
Abdomen	dorsal	7	15	16
	ventral	7	14	15

It will be seen that while there is little difference, if any, in cuticular thickness between the two Myrmica species, there is a marked difference between Formica and Myrmica. This difference in cuticular thickness could have a physically protective and/or thermoregulatory function. To investigate the former, specimens of Formica and Myrmica were subjected to a rough crushing test by confining individual ants under a watchglass and gradually adding weights until severe crippling and death occurred. It was found that, on the average, a weight of 365-405 grams was required to completely incapacitate M.rubra and M.scabrinodis, but F.lemani succumbed to 85 grams. Thus the protective qualities of the thicker Myrmica cuticle are very real. It might be suggested, therefore, that this thicker cuticle gives Myrmica protection against grazing animals as it is more likely to suffer from trampling due to its slower rate of travel and the consequent difficulty of taking avoiding action, whereas Formica, with its fast movements, may be better able to avoid a descending hoof. Again, it may be pointed out that Formica usually nests under some protective cover, whereas Myrmica is capable of building a nest up into an insolation area in quite an exposed position. While the adults of Myrmica are better protected from crushing, the larvae and pupae of

Myrmica do not, of course, have the same advantage.

It is felt by the writer, however, that any of the above advantages or disadvantages conferred by cuticular thickness may be mainly incidental ones, and that the main significance of the difference in thickness lies in thermal insulation.

The question of the thermal effect of difference in cuticular thickness is, in this instance, linked to the effect of cuticular colour, and is difficult to separate from it since the cuticle of F.lemani is much darker and melanic than is the cuticle of Myrmica which is typically of a reddish-brown colour. It was, however, shown experimentally that Formica gains and loses heat more rapidly than Myrmica. The following method was employed:-

Extremely fine thermocouples were made by arc-welding the thinnest copper and constantan (a cupro-nickel alloy) wires available. The thermojunctions were inserted either into the amputated abdomen of specimens of F.lemani and H.rubra, or into the thorax after removal of the abdomen. This insertion of the delicate thermojunction was carried out under a dissecting binocular microscope. After insertion, the point of entry was sealed with ester-wax in order to avoid interference with body temperature due to evaporation of body fluids (Waterhouse, 1951). In order to provide a direct comparison between Formica and Myrmica, one thermojunction of a pair was inserted in an F.lemani abdomen or thorax, and the other in a H.rubra abdomen or thorax, as appropriate. A Pye "Scalamp" reflecting galvanometer was used to indicate direction of flow of current. The two specimens were placed very close to one another in order to minimise any possible

extraneous effects due to convection. An electric heater, an infrared lamp and an opalescent light bulb were used as sources of radiation (sunlight was not available at this time). The trial was repeated using three different thermocouples with several ant specimens each.

In all cases the galvanometer indicated a faster increase in temperature of Formica than of Myrmica when the radiation source was switched on, and a corresponding slightly quicker loss of heat when the radiation source was removed.

It may be appropriately mentioned here that the cuticular surface of Myrmica is much smoother and shinier than that of Formica which is shagreened and of a matt appearance due to minute corrugations. Since radiation and absorption of heat are surface phenomena this would appear to be an additional insulating factor in Myrmica's heat economy, and Formica is, therefore, closer to a theoretical "black body" both in colour and surface texture.

6.3 Transmissivity of cuticle over the visible range of the spectrum.

In order to investigate further any cuticular differences which might be of significance in thermal economy, the transmissivity of Formica lemani and Myrmica rubra cuticles to light were compared over the spectral range 0.4μ to 1.0μ, i.e. the visible range and near infrared. The method employed was as follows:-

Small rectangles of integument were cut from the dorsal side of the abdomen in specimens of workers of the species being compared. The adhering hypodermis of these rectangles was

removed by scraping in distilled water under a dissecting binocular. The rectangles were then rinsed in distilled water, dried on blotting paper, and mounted on ordinary 3" by 1" glass slides, one for each cuticle type, to form large composite rectangles. The rectangles were held in position by an extremely thin smear of vaseline, and were fitted together under a dissecting binocular to ensure that no gaps existed between the constituents of the large rectangles. The outer cuticular surface of the constituent pieces was placed uppermost. Large flat areas of the two cuticles were thus built up, the size of which was determined by the size of the slits in the Unicam "S.P. 600" spectrophotometer by means of which the transmissivities of the cuticles were to be compared. In comparing the specimens by means of the above instrument, the H.rubra cuticle, having the highest transmissivity as determined by preliminary trials, was placed in the reference beam and the F.lemani cuticle in the test beam. This enabled direct comparison of the two cuticles at any particular wavelength. The outer cuticular surface of the specimens faced the beam source.

The results obtained are expressed graphically in Fig. 30. From this it can be seen that, under the test conditions, F.lemani cuticle only transmits 8% to 40% of what is transmitted by H.rubra cuticle over the visible range (roughly 0.4μ to 0.8μ). The relative transmission is least at the violet end of the spectrum and rises steadily to the red end. This trend is continued into the near infrared. It may be pointed out that the greatest intensity of solar radiation is at 0.475μ, and that about half the sun's radiant energy is dissipated in the visible region of the spectrum, the rest being divided between ultraviolet

and infrared.

The incoming radiation economy of any given body is governed by the three factors of reflection, absorption and transmission. Since Myrmica cuticle reflects more light than Formica over the visible range (it is lighter in colour to the eye, and has a much shinier surface as already noted), and since Myrmica cuticle also transmits more energy in the visible range as shown above, it follows that its absorption must be less, therefore F.lemani cuticle would be expected to stop more energy and so heat up more than M.rubra cuticle given the same amount of incident radiation at any wavelength in the visible spectrum. This high stopping power is, moreover, concentrated in a much thinner layer than in Myrmica which greatly facilitates re-radiation to cooler surroundings. This is in accordance with the thermocouple measurements already described.

6.4 Transmissivity of cuticle in the infrared.

As an extension of the above observations in the visible part of the spectrum, samples of cuticle from F.lemani and M.rubra were subjected to analysis by recording spectrophotometer over the infrared range 2μ to 15μ. Due to limitations of the measuring instrument, direct quantitative comparisons of the cuticles could not be carried out in the same way as in the visible range described above. Qualitative measurements were therefore carried out on each of the two cuticle samples separately. The method was as follows:

Fifty specimens of workers of each species were killed, the head and legs removed, and the abdomen and thorax opened under a dissecting microscope and scraped clear of contents, hypodermis and muscle attachments.

They were then rinsed in distilled water and again examined. After a final thorough rinsing in distilled water, the cuticle was superficially dried, then ground in an agate mortar. The resulting fine powder was dried in vacuo (about 1mm of Hg) for sixty hours at 20°C. Samples were then suspended in "Nujol" and analysed on the recording infrared spectrophotometer of the Chemistry Department, University of Glasgow, with the kind assistance of Dr. Iglinton of that Department.

The curves obtained are shown in Figs. 31 and 32. From these it will be seen that differences in qualitative transmission between the two species are negligible, and that the greater melanic content of the Formica cuticle does not appear to modify the transmissivity of the cuticle over this range of wavelengths. Both cuticles have marked "windows" just above 2.5μ, between 3.6μ and 5.9μ, and between 10μ and 15μ. They are relatively opaque to radiation between 2.9μ and 3.6μ, also 5.9μ to 10μ.

Any differences between the two cuticles over this range of wavelengths would appear, therefore, to be purely quantitative due to the difference in thickness and surface characteristics. It is interesting to note that the above curves obtained for Formica and Myrmica are broadly similar to those shown by Richards (1951) for Periplaneta and Rhonnia.

6.5 Discussion

The purely physiological consequences of the colour of the integument of insects, and, indeed, of all animals, have hitherto been considered by a surprisingly small number of authors. This situation appears to have arisen out of the emphasis which has been placed on the importance of the evaporation of moisture

in the control of body temperature. While the importance of the latter is not disputed, it is felt that the relationships between body colour, radiant energy and body temperature are of more significance than the number of workers in this field would seem to imply.

Uvarov (1931) provided an excellent summary of the situation as it was at that time, and there does not appear to have been much important work done since then. To quote the latter author, "These observations (Dodenheimer, 1930) show the importance of the coloration of insects in their thermal economy. This problem has been much neglected by the numerous students of insect coloration, who have regarded the latter as a character of certain evolutionary value, but not as a physiological factor of great importance".

Lord Walsingham (1885) appears to have been one of the first workers to discuss the importance of dark coloration in the thermal economy of insects, which he demonstrated by his famous experiment of laying black and white lepidoptera on the surface of snow. He inferred that a dark insect was better able to make use of short periods of sunshine, while a light coloured one would still be inactive due to low body temperature.

Burton (1923) was among the first to draw attention to the high incidence of black pigmentation in diurnal desert birds and insects, and confessed himself at a loss to account for this, as it seems to be a bad adaptation for desert animals on account of increased absorption of heat. Dodenheimer (1954) discusses the same apparent paradox and concludes that there must be reasons for this which we are at present unable to recognise. He also suggests that the black colour may be the

consequence of raised melanin production as a reaction to certain parts of the solar spectrum.

There is also a high percentage of dark-coloured nival animals. Collembola living on the snow in the alps are always black (Handschin,1919; Parker,1921; Vorbrodt,1922; Hani, 1962). Pearsall (1950) remarks on the fact that "Dark and dingy colours are often characteristic of mountain insects", also mountain spiders.

On consideration of the above mentioned habitats it becomes clear that one important factor common to all is a high intensity of solar radiation. In the case of mountain tops this is due mainly to the fact that the amount of solar radiation reaching the earth's surface increases with height above sea level (Horikofer,1935; Lauscher,1937). Increased reflection from rocky surfaces may also play a part. As regards nival regions, those at high altitudes will have a two-fold increase of radiant energy above the snow. Besides the increased insolation due to increase in altitude as described above, there is also an enormous amount of reflection from the snow surface, which may amount to 85% of the incident energy in both the ultraviolet and visible parts of the spectrum. In the infrared, however, snow is practically a "black body" with a reflection of only 0.5% (Coblentz, 1926; Lauscher and Sekal,1931; Bartels,1930; Falckenberg,1928). So that while ultraviolet and visible intensities are greatly increased by reflection, there is practically no increase in infrared. On the sea shore intensity of radiation is increased by reflection from the sand (ultraviolet 8-17%, visible 37%, infrared 11%), and, to a lesser extent, from the surface of the sea (8-10% in the visible region),

(Buttner and Buttner,1935; Voigts,1938; Falkenberg,1928). In deserts, also, radiant energy is increased by reflection from sand and rock.

A small number of authors have worked on spectral reflectance and transmissivity of insect cuticles. Richards (1954) gives infrared "absorption" curves for pronota of Periplaneta americana and for the larval cuticle of a blowfly. Parker (1939) gives data for beetle elytra over the ultraviolet and most of the visible spectrum, and demonstrates the importance of structure as well as colour. Duspiva and Ozeny (1934) claim that darkly pigmented cuticles are heated more by visible light than by infrared, and Richards (loc.cit.) states that the latter "may be presumed to penetrate better than visible light".

With reference to the human species, Weiner (1954) states "Yet another problem is the significance to be allotted to melanin pigmentation of the skin". Ladell (1957) puts forward the classical point of view that a pigmented man is less susceptible to sunburn owing to the protective effect of melanin against ultraviolet radiation, and states that the pigmented skin absorbs more of the other radiation as well. He goes on to say that a white man reflects three times as much direct incident solar radiation as does a black man, but both absorb the same amount of low temperature radiation (i.e. long wavelength infrared) from the ground. In an attempt to elaborate further the possibility that a dark integument might have a greater emissivity of heat than a non-pigmented integument, the writer carried out a short and relatively crude experiment on human skin in 1955. The method was as follows:

A simple thermopile was made, consisting of

14 copper/constantan junctions in series. The seven "hot" junctions had circular copper discs soldered to them, the receptive surface of the copper being blackened in a sooty flame which also gave a matt surface. The "hot" junctions were arranged in the form of a rosette in a cardboard cylinder which protected them from convection. The "cold" junctions were insulated, placed in a stoppered tube and kept in a thermos flask of ice when in use. The current generated was measured by a mirror galvanometer. The subjects were seated with their head in a clamp, and the cardboard cylinder placed opposite, and at a fixed distance from, the upper cheek, which thus radiated along the cylinder to the thermojunctions at the other end. The following results were obtained (read in arbitrary units since the instrument was not calibrated):-

Subject	Clinical Thermometer(°F)	Galvanometer Reading
1. West African	96.4	139
2. British	96.6	128
3. West African	98.4	136
4. British	97.4	122
5. West African	97.5	136
6. British	97.8	128
7. West African	98	137
8. British	98	116
9. Ceylonese (Tamil)	97	134
10. British	97.8	127

Harrison (1964), in an interesting review of the subject, agrees that the human skin, regardless of its colour, radiates heat at near maximum efficiency. He points out, however, that in all

the experiments dealing with the subject there appears to be a consistent tendency for black skin to have a slightly greater conductivity than white skin. He states - "The difference is certainly small, but it does not follow that the biological effect will also be small. There can be no doubt that in equatorial forests, where the atmosphere for most of the day is nearly saturated, and little metabolic heat can be lost by the evaporation of sweat, radiation must be an important factor in thermoregulation". This point of view is therefore in agreement with the indications obtained by the rather limited experiment described above.

Thus while it is generally agreed that an important role of dark coloration is that of a protector of the internal organs from excessive ultraviolet damage under conditions of comparatively intense radiation, and also enables maximum absorption of available solar energy thus enabling an increase in metabolic rate and faster movement, it should also be remembered that a black integument is an efficient radiator of body heat. This radiant heat loss may be extremely important from an adaptational point of view, especially so in a humid atmosphere where the opportunity for loss of heat by evaporation of water will be greatly reduced, and among insects where loss of body moisture cannot be employed economically as a temperature controlling device in most cases. The importance of the radiation characteristics of the integument is thereby increased.

6.6 Summary

(a) The cuticle of Formica adults was shown to be much thinner than that of Myrmica.

(b) Myrmica adults are, in consequence, much better protected from crushing or trampling than is Formica.

(c) The cuticle of Formica is, however, darker and more melanic than that of Myrmica, therefore it is difficult to relate any differences in the thermal economy of the species to differences in cuticular thickness alone.

(d) Formica, however, tends to gain and lose heat more rapidly than Myrmica.

(e) The cuticular surface of Myrmica is much smoother and shinier than that of Formica which is shagreened and of a matt appearance due to minute corrugations. Since radiation and absorption of heat are surface phenomena this is an additional insulating factor in Myrmica's heat economy.

(f) F.lemani cuticle transmits only 8% to 40% of the energy transmitted by M.rubra cuticle over the visible range. The relative transmission is least at the violet end of the spectrum and rises steadily to the red end.

(g) The qualitative transmissivities of F.lemani and M.rubra cuticles in the infrared are practically identical. There is thus no obvious differentiating factor operating over this part of the incoming spectrum.

(h) The significance of the darker, thinner and rougher cuticle of F.lemani therefore appears to be expressed in:

(i) protection from ultraviolet,

(ii) maximum absorption of available insolation, and

(iii) the possibility of rapid elimination of excess body heat in a humid environment or under conditions where body fluids cannot be spared for evaporative cooling.

7. Thermal properties of the rock-types used in heat-site accumulation experiments.

7.1 Introduction.

The field observations on the temperature regimes under the various rock-types used in the colonisation experiments were supplemented by some more detailed considerations of the thermal properties of these rock-types. The whole question of the factors involved in the absorption, conversion and transmission of solar energy, i.e. the mechanics of insolation, is of great interest, and some aspects of this which are applicable to the present investigation may be briefly mentioned.

7.2 Reflectance values.

Beginning with the question of absorption of solar energy by the three different rock-types used (viz., sandstone, basalt and slate), it was considered that the amount of energy absorbed by the units would be determined by the reflectance of the various surfaces, i.e. the part of the incident radiation which was not reflected from the surface would be absorbed and converted to heat. The units were so thick and opaque that any direct transmission could be ruled out, at least over most of the incoming spectrum, and certainly near the wavelengths of greatest energy.

Accordingly, it was decided to compare the reflectances of the three rock-types over the visible range of the spectrum,

i.e. including the peak of incoming energy. The method was as follows:-

Discs of the three rock-types were cut to a suitable size, that of the slate being perpendicular to the cleavage, and their reflectances measured on a Unicam "S.P. 540" spectro-photometer with diffuse reflectance attachment. The disc reflectances were compared with a magnesium carbonate standard. The measurements were made possible by courtesy of the Technical Liaison Department of Unicam Instruments Limited, Cambridge. The results are shown in Fig. 33 .

Basalt showed a steady reflectance of about 7% over the whole range (.35μ to .7μ) and is the "blackest" body of the three types. Sandstone showed a steady increase in reflectance with increasing wavelength, reflecting twice as much in the near infrared as it does in the near ultraviolet. Slate, on the other hand, showed a fluctuating reflectance over the range measured, having a maximum reflectance in the middle of the visible spectrum, as might be expected from its greenish colour. The indications are, therefore, that basalt absorbs more solar radiation over the visible range than either slate or sandstone. The latter appears to absorb more than slate, taking the visible spectrum as a whole, and slate certainly reflects more of the maximum-energy wavelengths around .5μ.

7.3 Heat capacity and heat diffusibility

After absorption of the solar radiation it is converted to heat, the resultant temperature of the absorbing body being determined mainly by its heat capacity, or mass multiplied by specific heat. The concept of heat diffusibility is also important since this is an indication of the facility with which

heat can be transferred within a particular solid.
Heat diffusibility is expressed by:-

$$\frac{K}{d \times s}$$

where K is conductivity
d is specific gravity
s is specific heat

The thermal properties of a variety of rock-types have been worked out by various authors. References are to be found in Reports of the British Association for the years 1878, 1881 and 1938. There are also relevant papers by Poole (1914) and Benfield (1939).

The following values for sandstone, basalt and slate are published in the above British Association reports:

	Specific Gravity	Specific Heat	Conductivity
Sandstone	2.14	.21	.0075
Basalt	2.7	.21	.0055
Slate	2.75	.21	.006 (perpendicular to cleavage)

The specific gravities of the rock-types actually used in the present work were estimated by means of a specific gravity bottle, using crushed rock specimens. The values obtained were:

	Specific Gravity
Sandstone	2.29
Basalt	2.7
Slate	2.65

Using these figures, and the published values for specific heat and conductivity as shown above, the heat diffusibilities of the three rock-types were calculated, giving the following values:

	Heat Diffusibility $\frac{K}{d \times s}$		
Sandstone:	$\frac{.0025}{2.29 \times .21}$	=	.0156
Basalt:	$\frac{.0055}{2.7 \times .21}$	=	.0097
Slate:	$\frac{.006}{2.65 \times .21}$	=	.0108

Similarly, the heat capacities of the units used were calculated (dimensions of sandstone and basalt 15 x 10 x 5 cms; of slate 15 x 10 x 1 cms):

	Heat Capacity (Volume x d x s)		
Sandstone:	750 x 2.29 x .21	=	360.68
Basalt:	750 x 2.7 x .21	=	425.25
Slate :	150 x 2.65 x .21	=	83.48

7.4 Discussion

The above values help towards an understanding of the thermal economy of the various rock-types, the diurnal temperature regime under units as measured in the field and also as to why sandstone was preferred to the other two rock-types by *F.lemani* and *H.scabrinodis* in the colonisation experiments.

Considering the three main factors of reflectance, heat capacity and heat diffusibility, sandstone would appear to

occupy an optimum position from the point of view of thermal economy of the underlying mass. Firstly, although it absorbs slightly less of the incident energy (in the visible range) than does basalt, it absorbs slightly more than slate and so may be regarded as intermediate in this respect. Secondly, the heat capacity of the sandstone units again places this rock-type in an intermediate position. Although not being able to store quite as much heat as basalt, it is a much better buffer than the slate units which have a relatively low heat capacity and exhibit rather sudden temperature changes. Thirdly, due to its higher conductivity and lower density, sandstone shows a much greater heat diffusibility than basalt, thus enabling a more rapid transfer of energy to the lower surface of the unit. Its heat diffusibility is also greater than slate, but due to the comparative thinness of the slate units this advantage would not be so marked.

7.5 Summary

(a) Some factors affecting the thermal economy of the rock-types used in the nest-appropriation experiments were briefly considered.

(b) Reflectances of the three rock-types were compared over the range .35μ to .7μ. This gave an indication of the comparative amounts of energy absorbed by each rock-type.

(c) Basalt absorbed more radiation over this range than either slate or sandstone. The latter appears to absorb more than slate, taking the visible spectrum as a whole, and slate certainly reflects more of the maximum energy wavelengths around .5μ.

(d) The basalt units had a higher heat capacity than the sandstone units, which, in turn, had a higher heat capacity than the slate units.

(e) Sandstone had the highest heat diffusibility, or property of heat transfer, slate was intermediate in this respect and basalt had the lowest value.

(f) It is concluded that the popularity of the sandstone units in the colonisation experiment may be explained by the fact that they have a more lively response to incoming radiation than basalt, due to their higher heat diffusibility, and yet a higher conservation of heat than the slate units due to their higher heat capacity. They also absorb more energy than slate at the wavelength of maximum incoming energy.

8. Synthesis

If to the differentiating factors described in the present account are added those described for the same species by Brian (1952a, 1952b, 1955), then one may begin to have a comprehensive view of some of the adaptations and limitations by means of which integration of the three main species in the ecosystem has been made possible.

Firstly, the differences described between Formica and Myrmica:

Physical	Behaviouristic
(a) Cuticular colour	(g) Diurnal activity maxima
(b) Cuticular thickness	(h) Nocturnal activity
(c) Cuticular surface	(i) Foraging range
(d) Cuticular transmissivity	(j) Speed of travel
(e) Parasitism by cestodes	(k) Foraging stratification
(f) Insulation of body temperature	(l) Ability to build mounds

Secondly, the differences described between M.rubra and M.scabrinodis:

Physical	Behaviouristic
(a) Base of antennae	(b) Foraging stratification
	(c) Agressiveness
	(d) Nest-site tenacity
	(e) Nest architecture
	(f) Tolerance of low humidities

The association with myrmecophilous aphids did not appear to play any major role in eco-differentiation.

Diagram Illustrating Possible Relationships of Some Eco-differentiating Factors

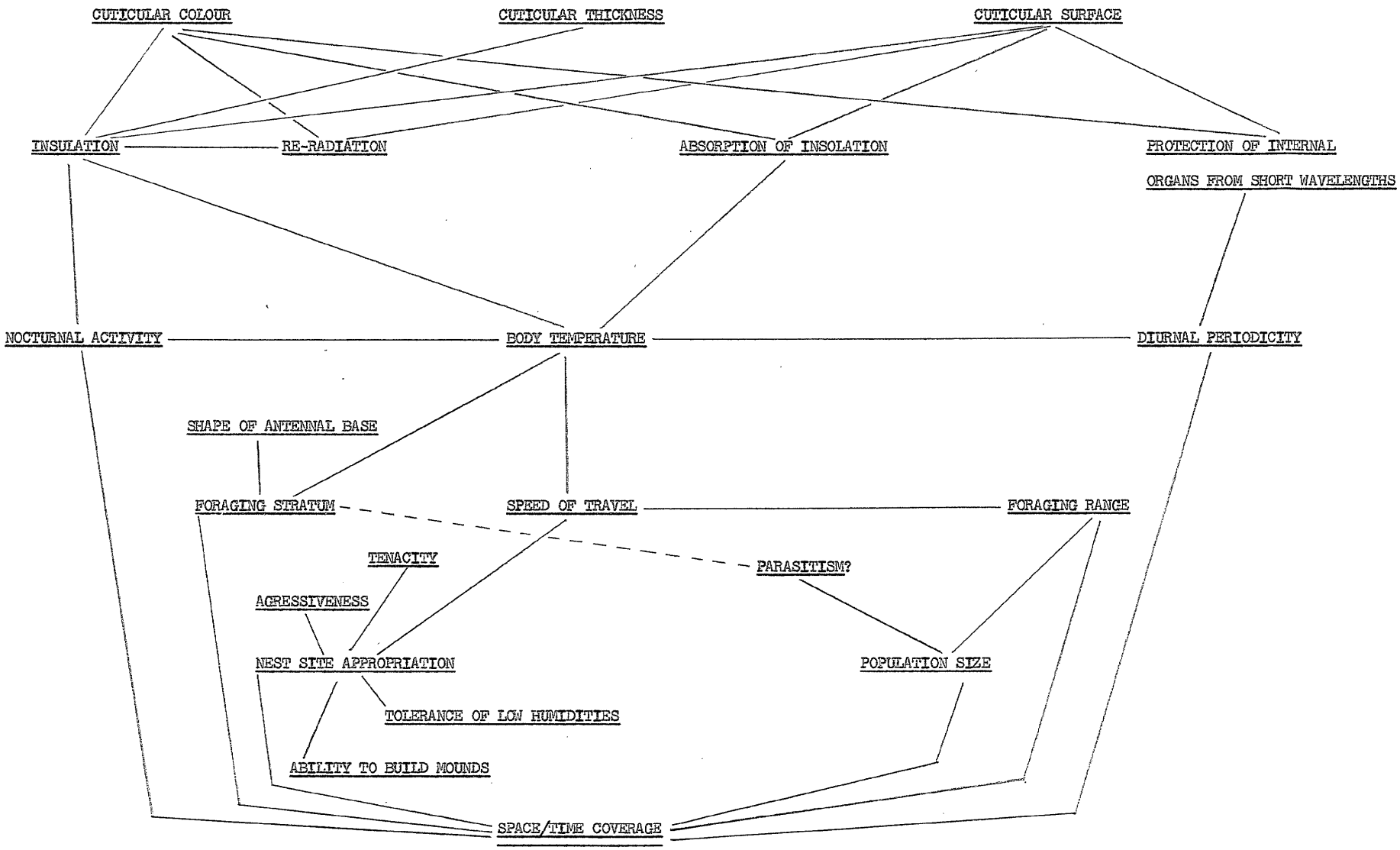

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Plate 1. The experimental area.

Plate 2. The experimental area, showing sites for the measurement of activity.

Plate 3. The experimental area, as above.

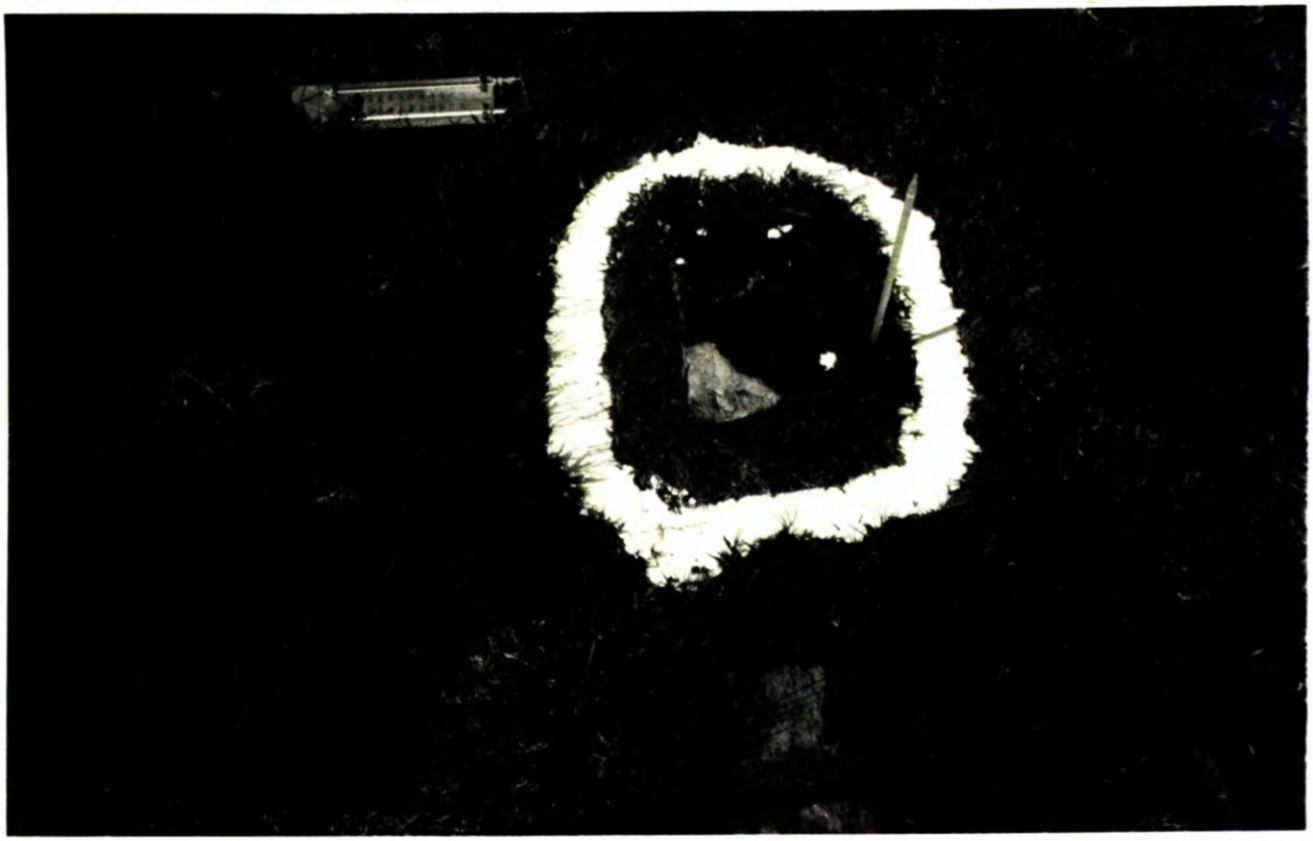

Plate 4. Nest ringed for measurement of activity.

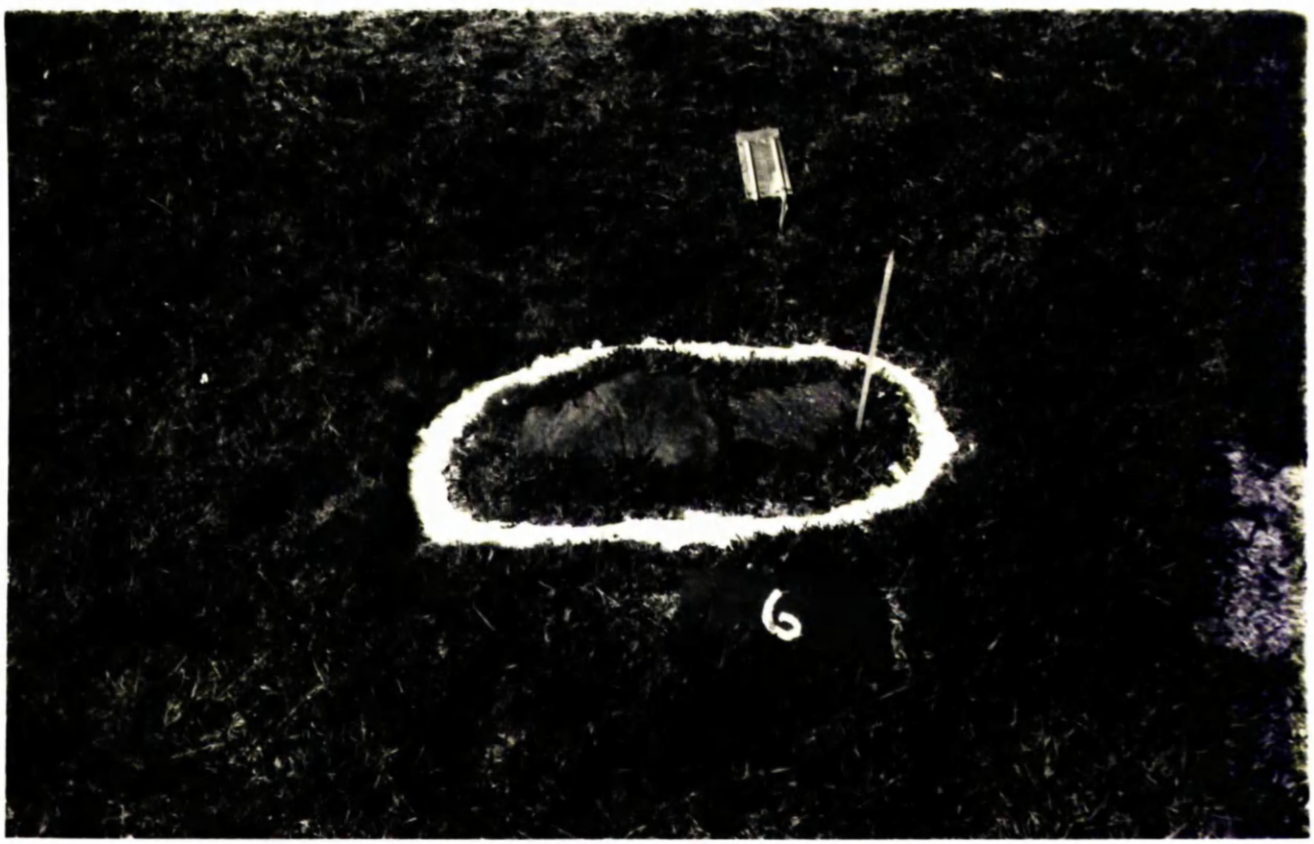

Plate 5. Nest ringed for measurement of activity.

Key:- Figs. 1 to 19

●——● Formica lemani

o——o Myrmica scabrinodis

✣——✣ Myrmica rubra

L——L Leptothorax acervorum

s——s Sandstone

m——m Slate

1——1 Basalt

FIG 1.

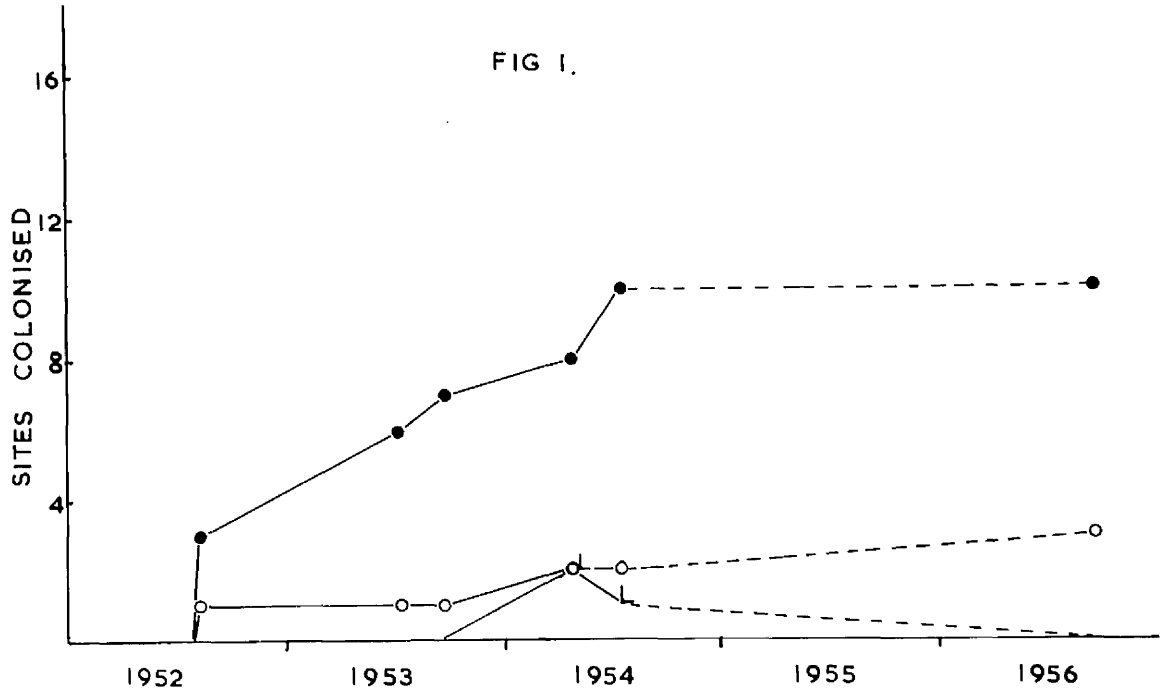

Fig. 1: Sandstone Quadrat (Open). Sites colonised by each species

FIG. 1A

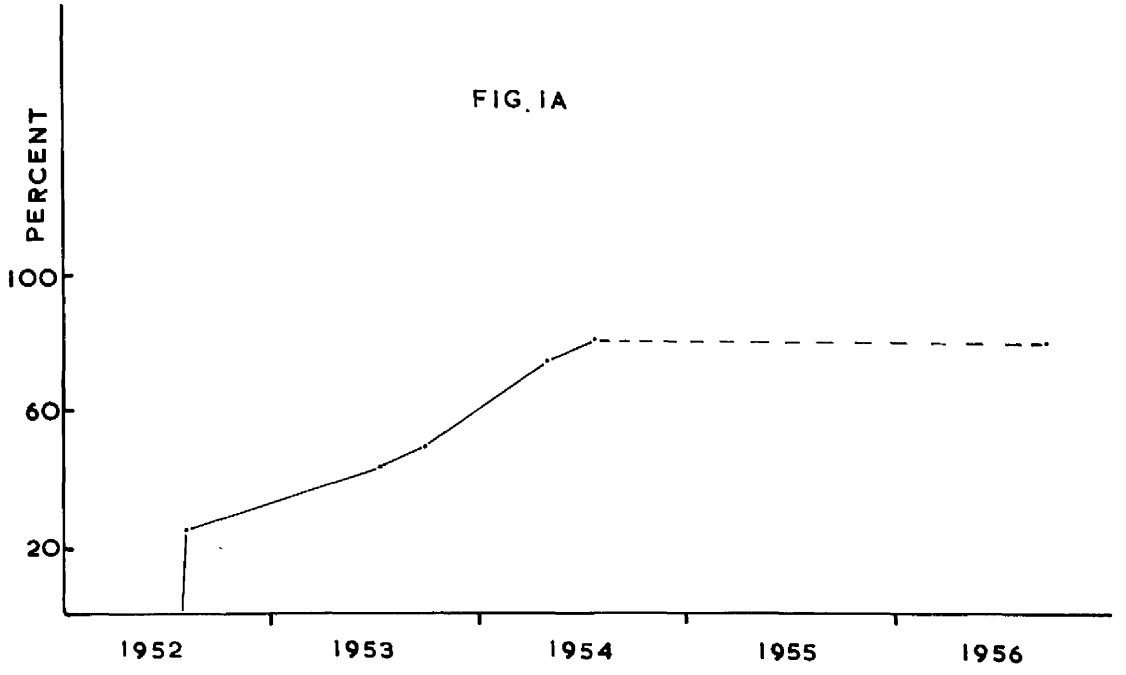

Fig. 1A: Sandstone Quadrat (Open). Total percentage colonised.

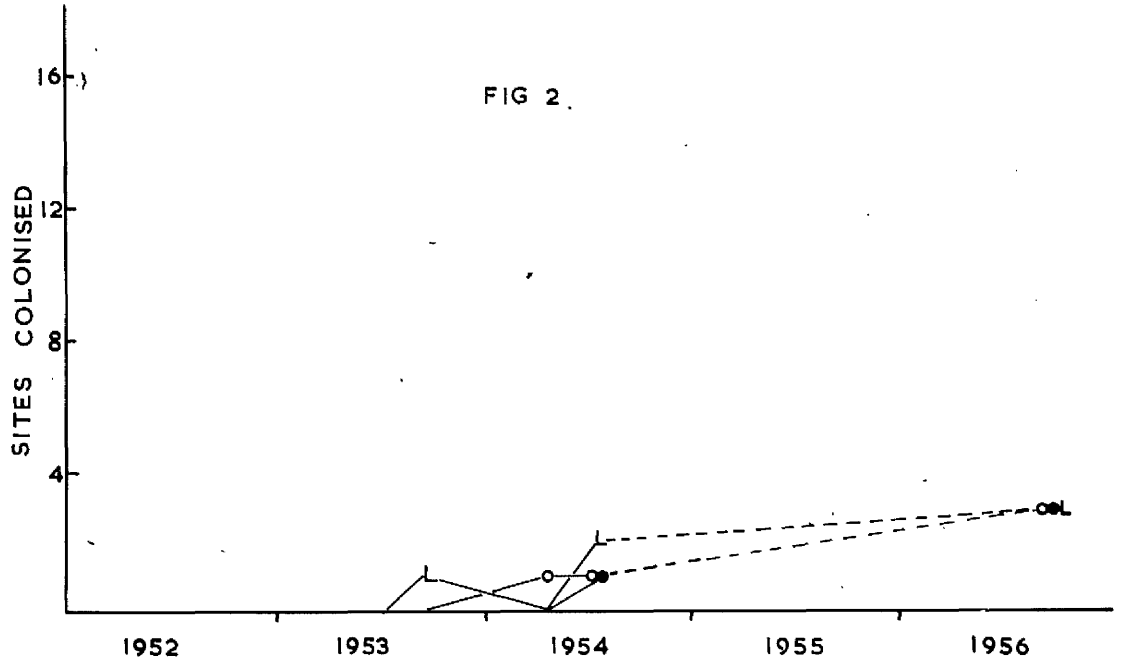

Fig. 2: Basalt Quadrat, Sites colonised by each species.

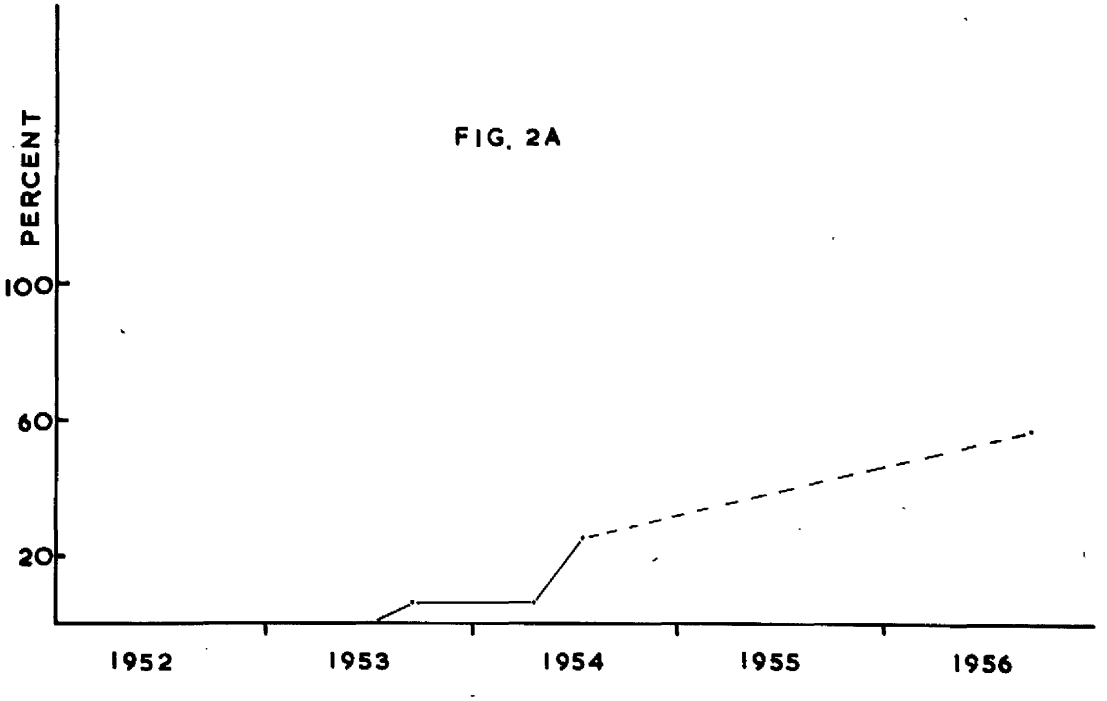

Fig. 2A: Basalt Quadrat, Total percentage colonised.

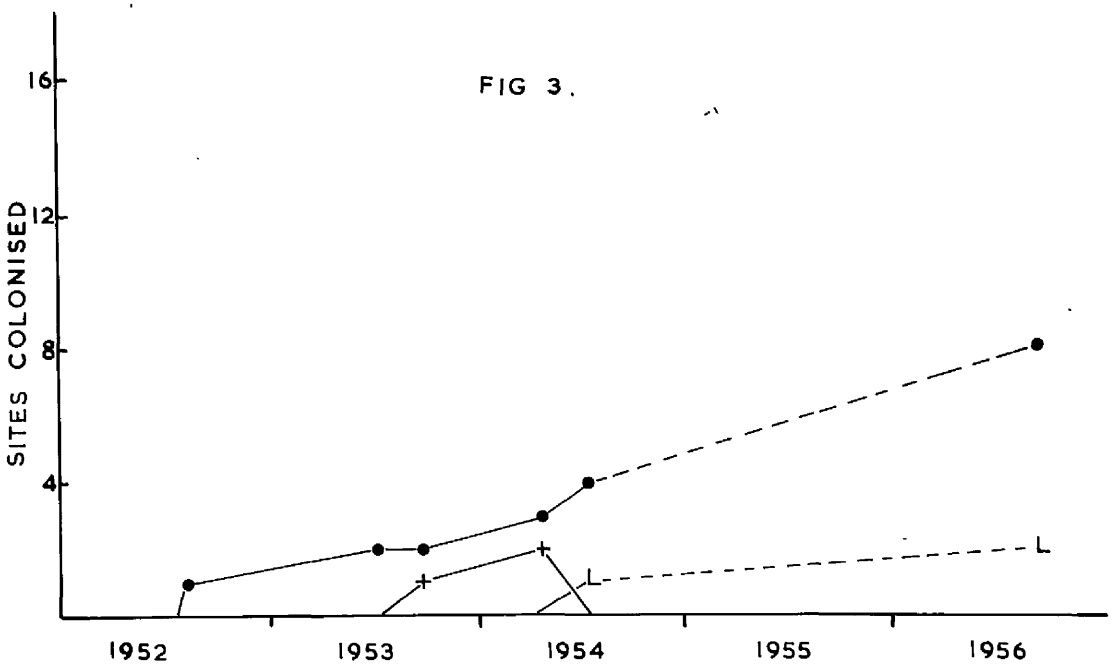

Fig. 3: Slate Quadrat, Sites colonised by each species.

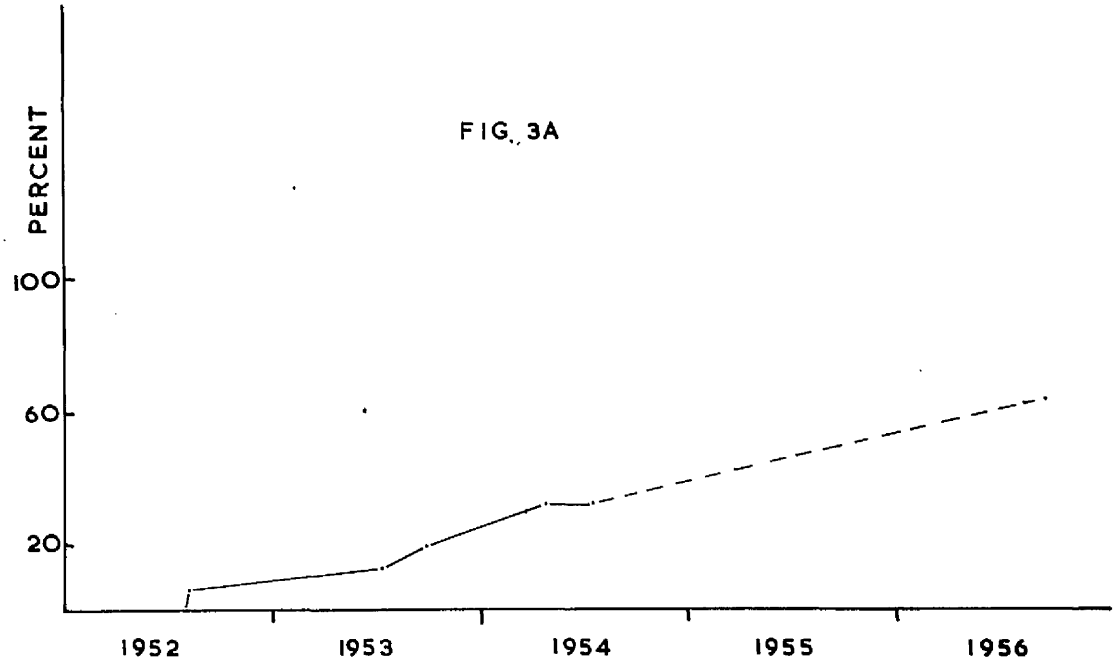

Fig. 3A: Slate Quadrat, Total percentage colonised.

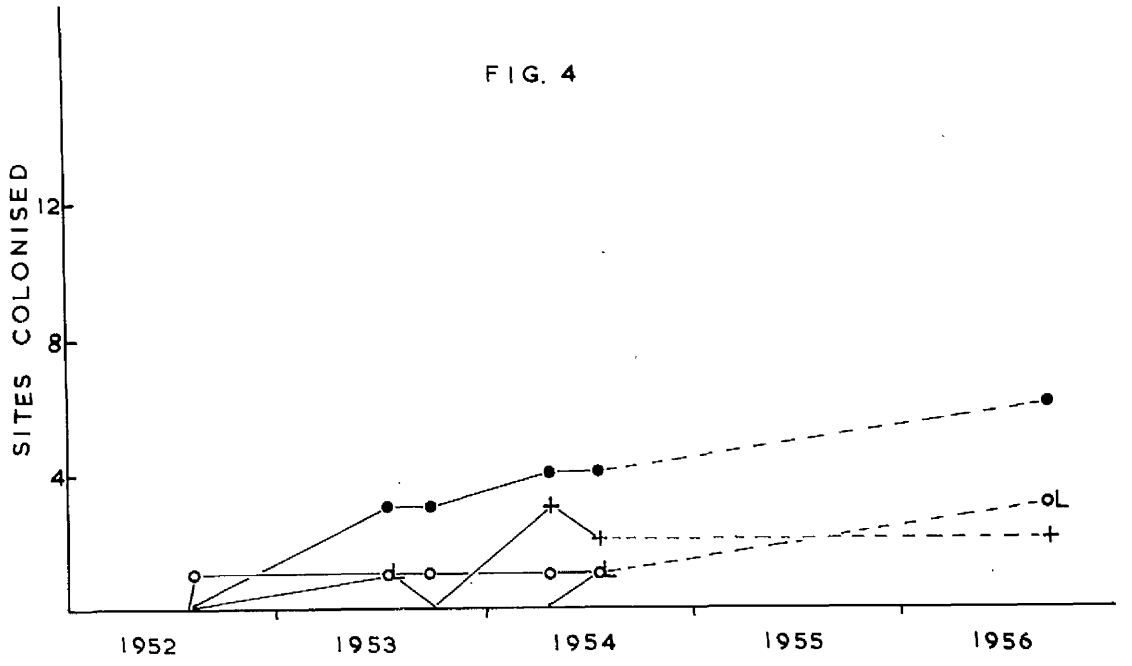

Fig. 4: Triplet Sandstone. Sites colonised by each species.

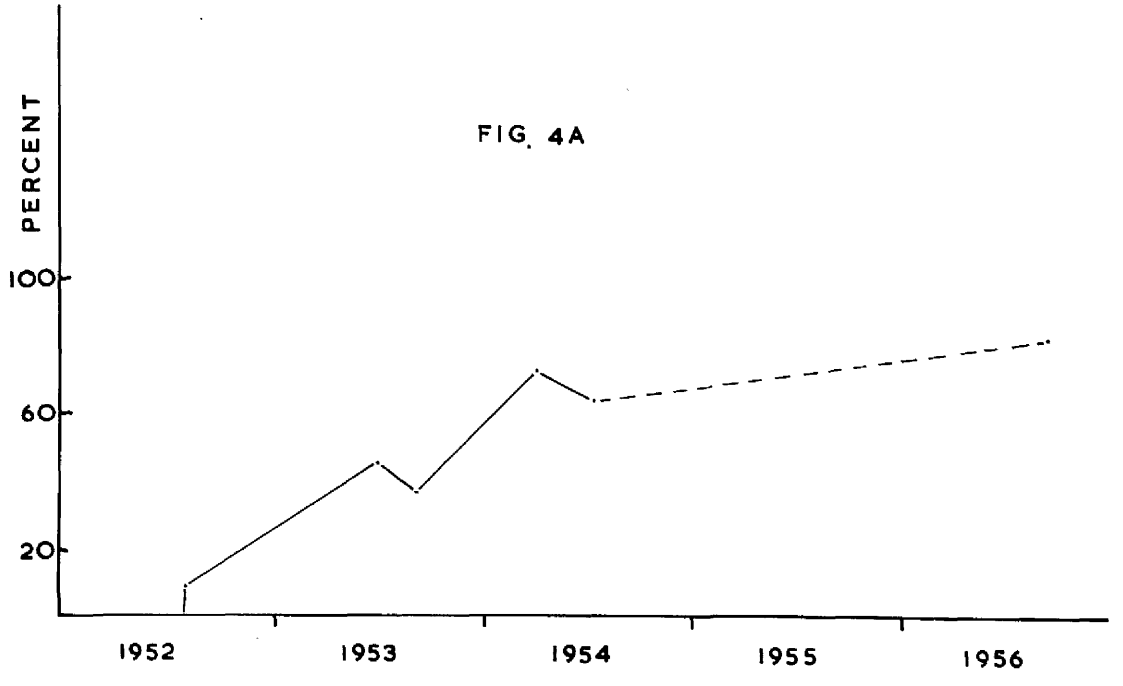

Fig 4A: Triplet Sandstone, Total percentage colonised.

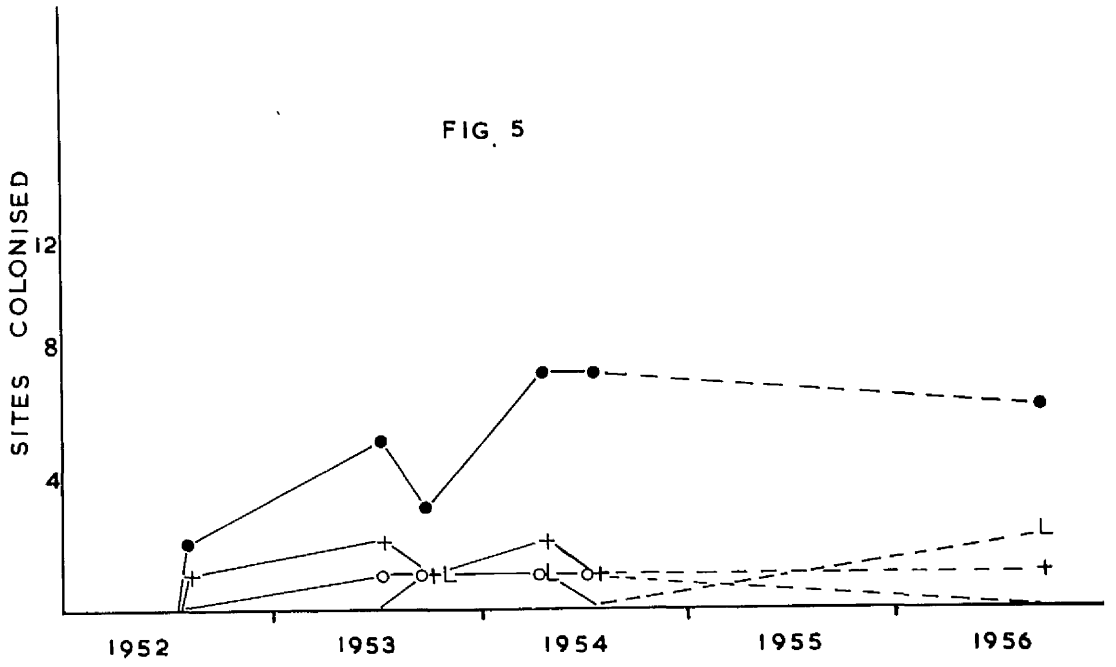

Fig. 5: Trinlet Basalt, Sites colonised by each Species.

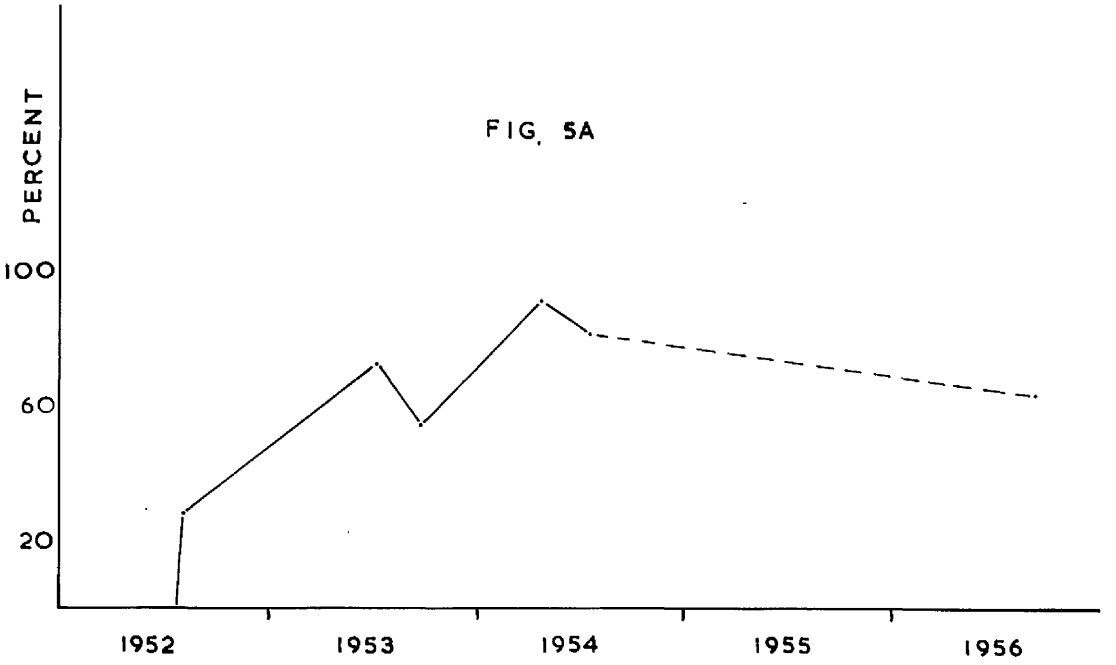

Fig. 5A: Trinlet Basalt, Total percentage colonised.

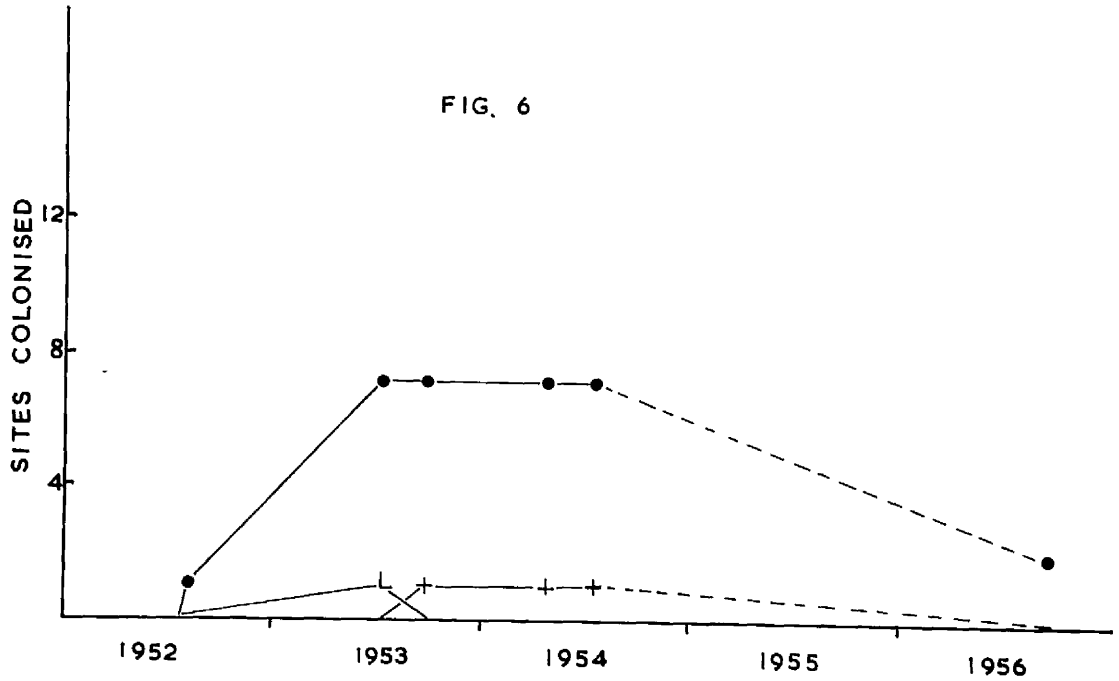

Fig. 6: Triplet Slate, Sites colonised by each species.

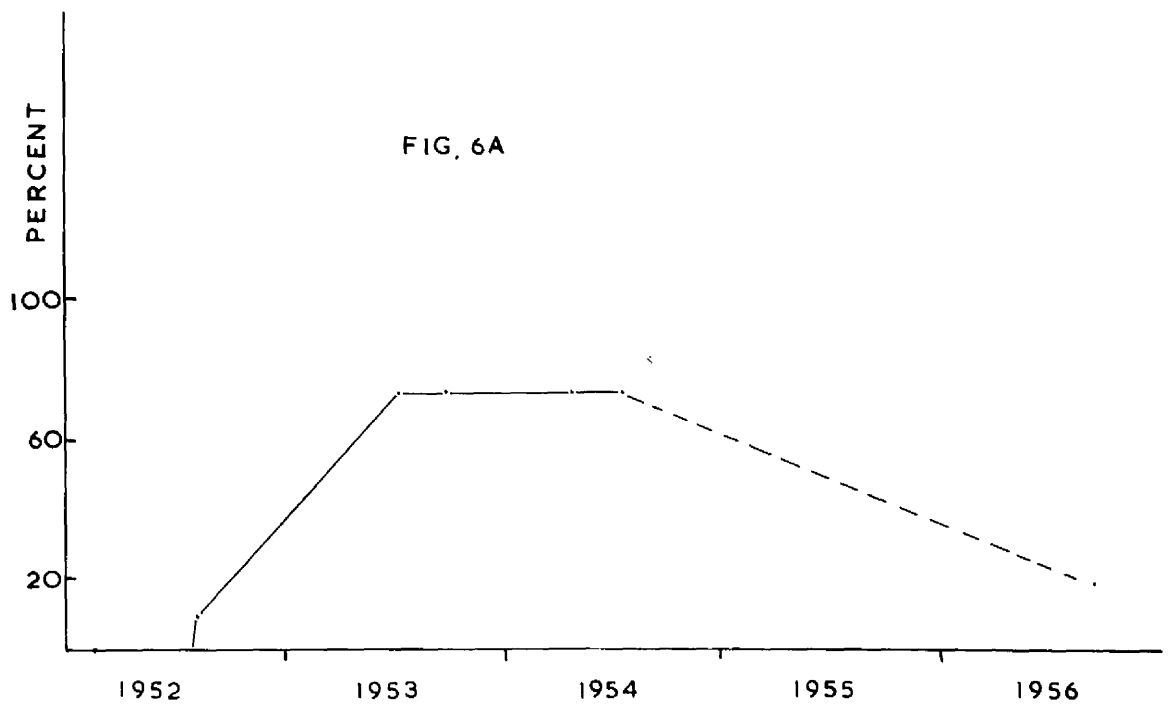

Fig. 6A: Triplet Slate, Total percentage colonised.

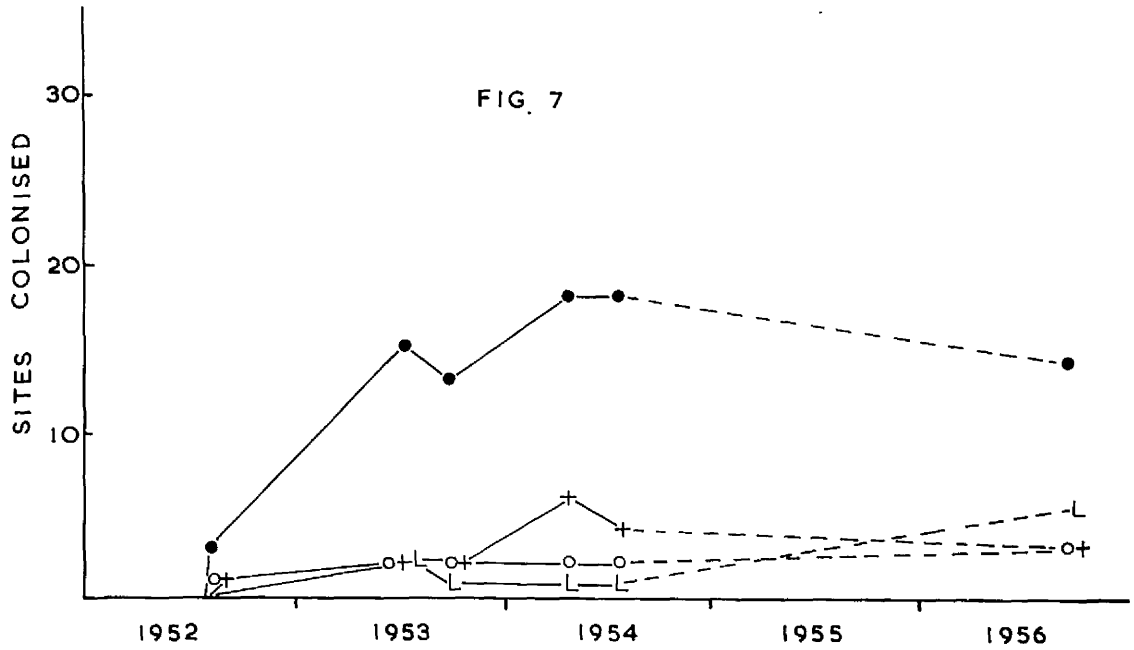

Fig. 7: Quadrat Totals: Sites colonised by each species.

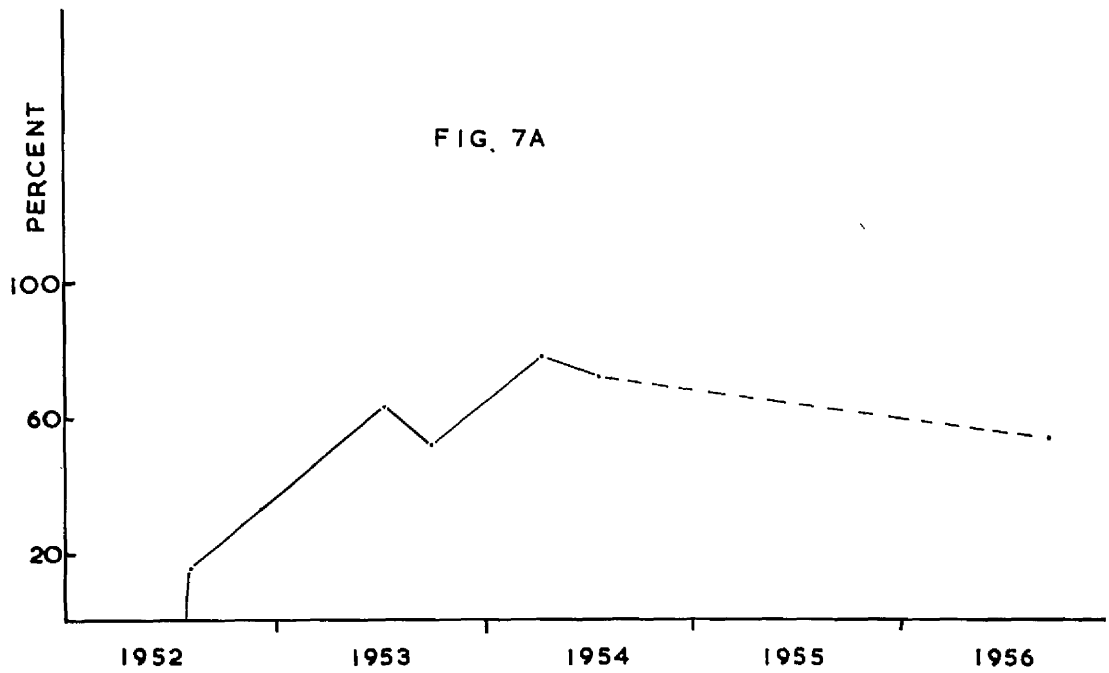

Fig. 7A: Quadrat Totals, Total percentage colonised.

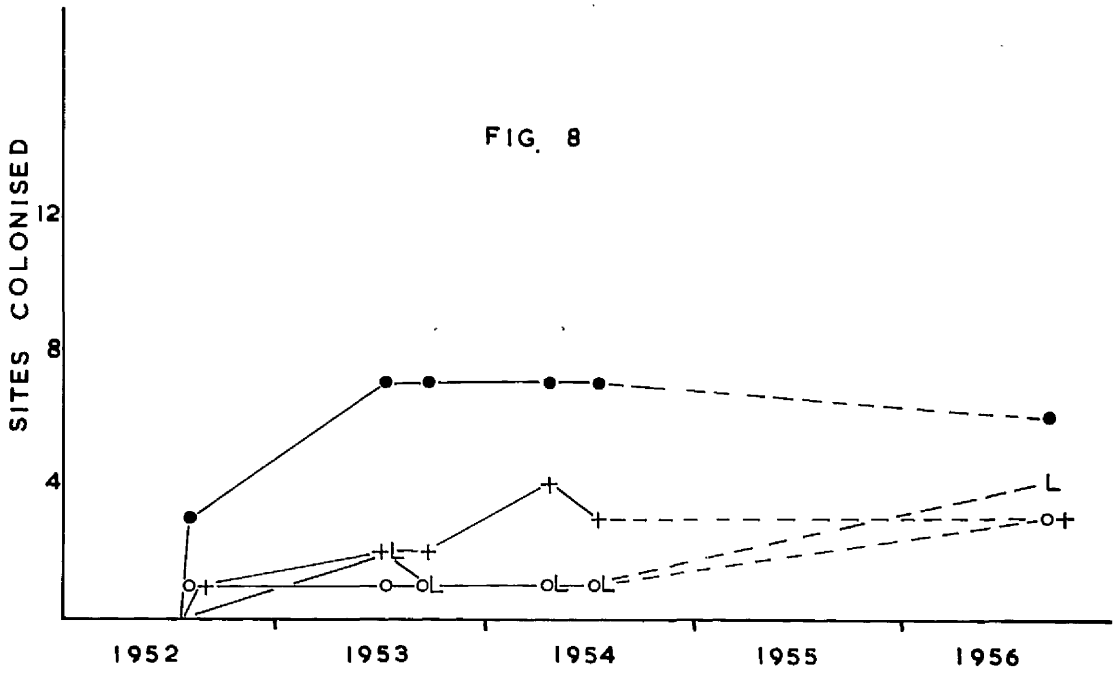

Fig. 8: Triplets (each considered as a single unit), Sites colonised by each species.

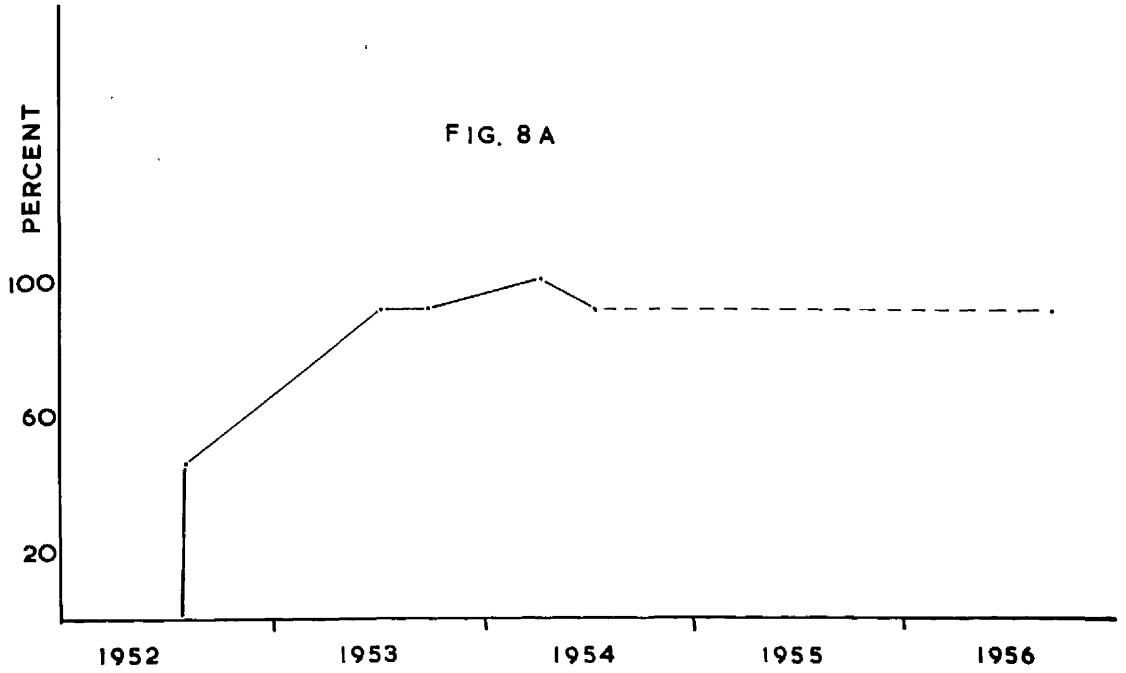

Fig. 8A: Triplets (each considered as a single unit), Total percentage colonised.

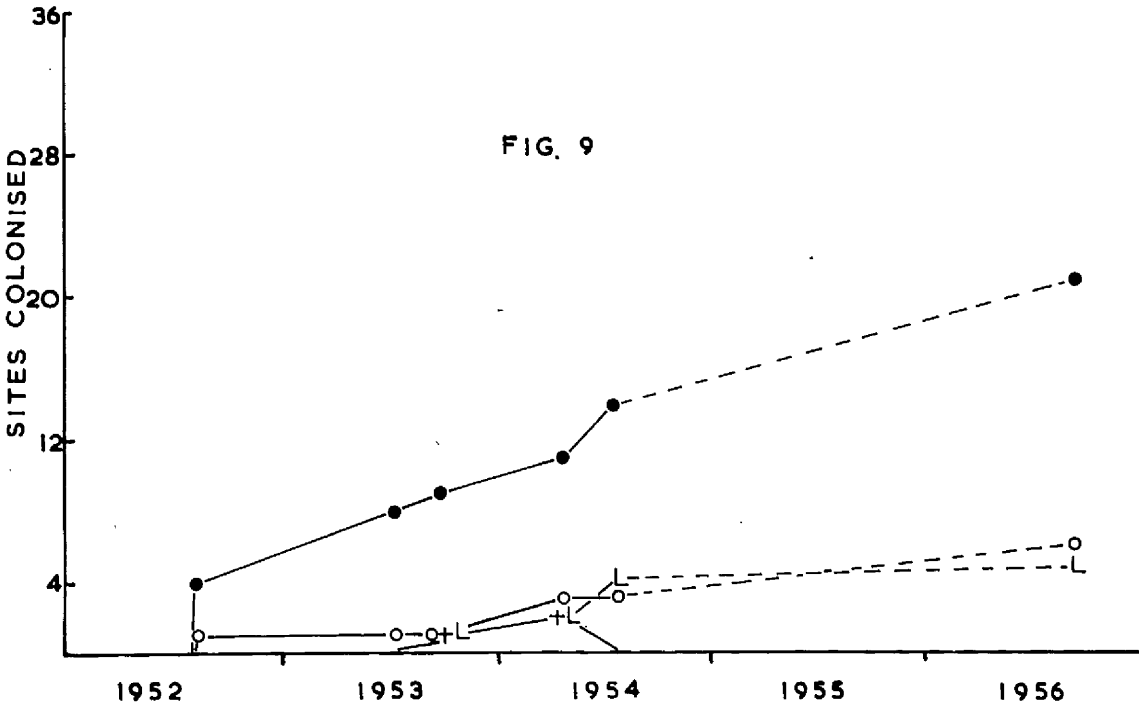

Fig. 9: Triplet Totals. Sites colonised by each species.

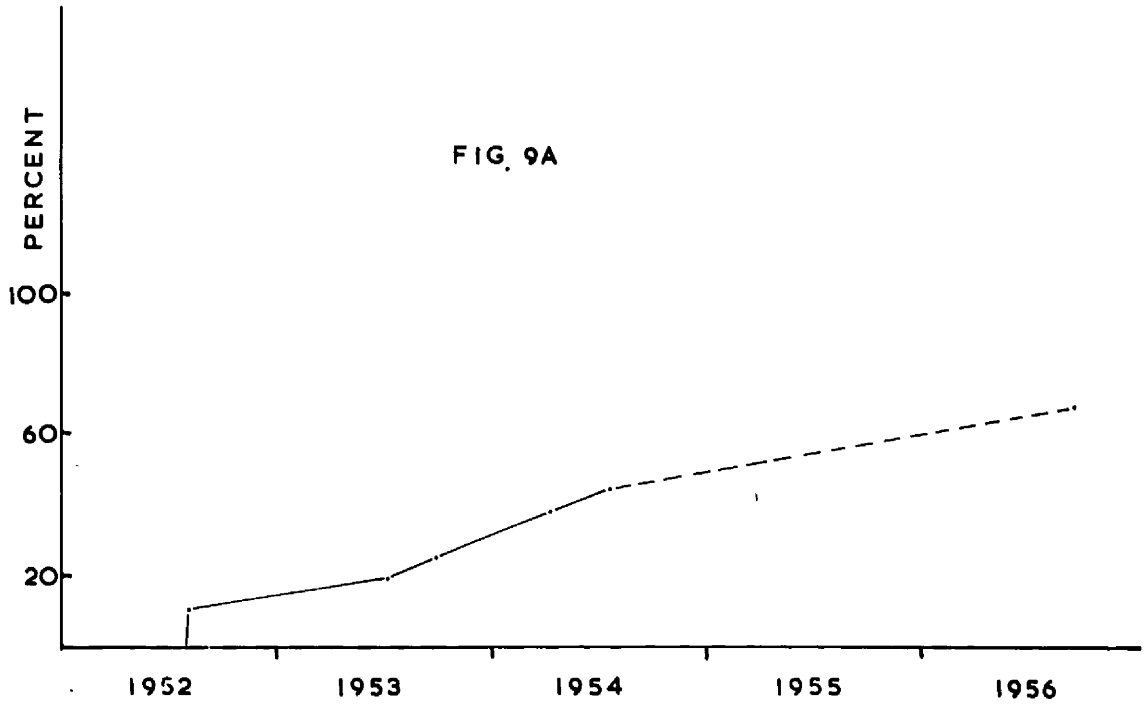

Fig. 9A: Triplet Totals. Total percentage colonised.

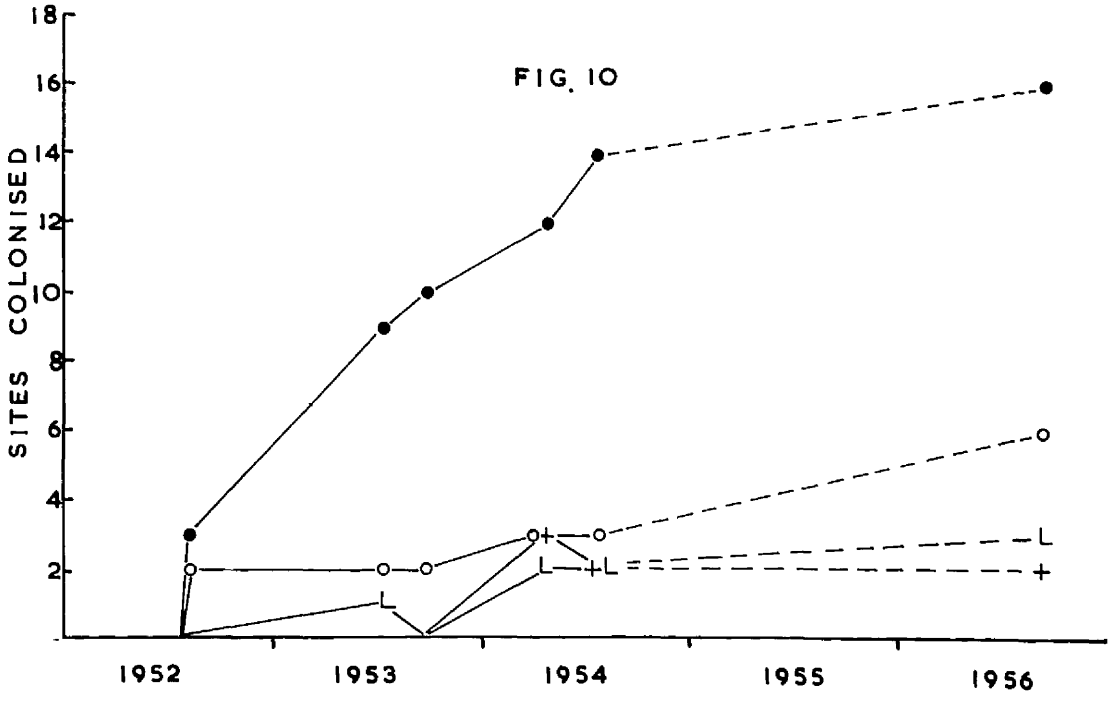

Fig. 10: Total Sandstone: Sites colonised by each species.

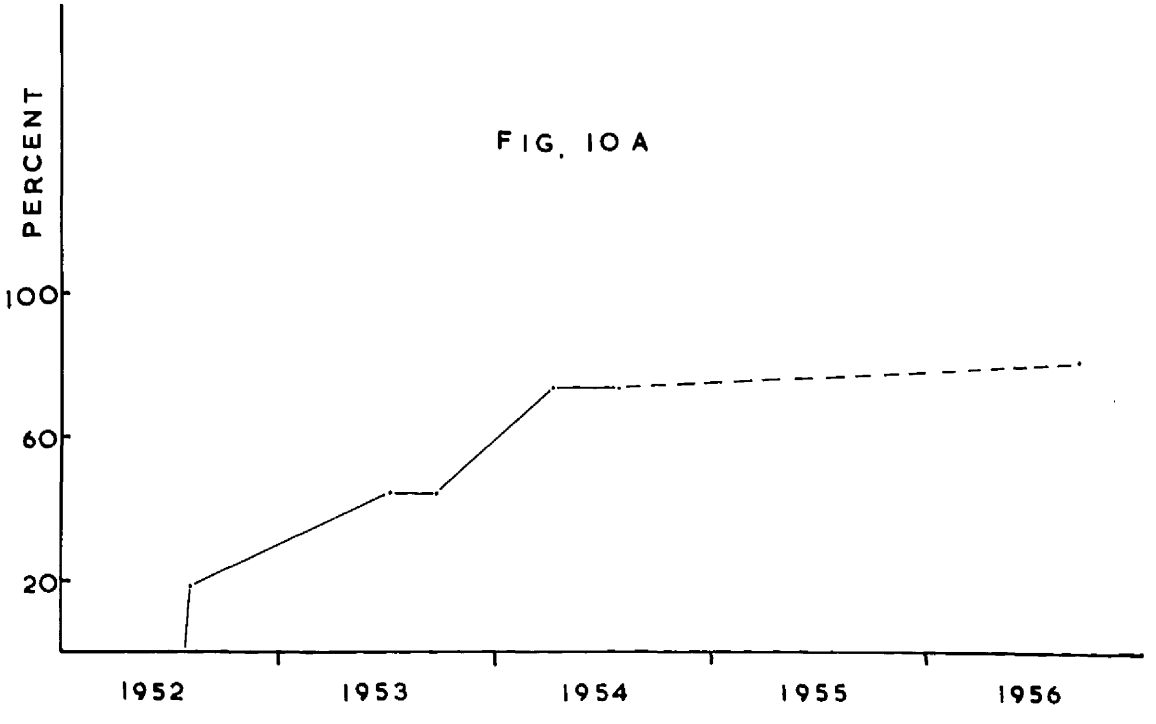

Fig. 10A: Total Sandstone. Total percentage colonised.

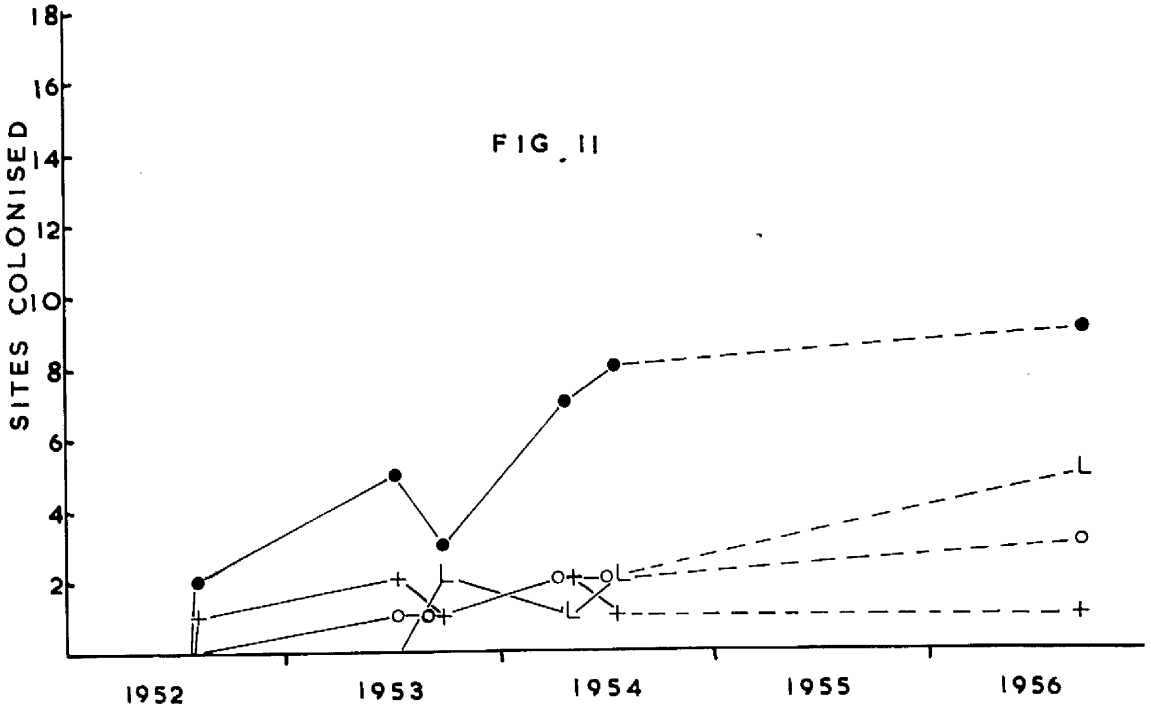

Fig. 11: Total Basalt. Sites colonised by each species.

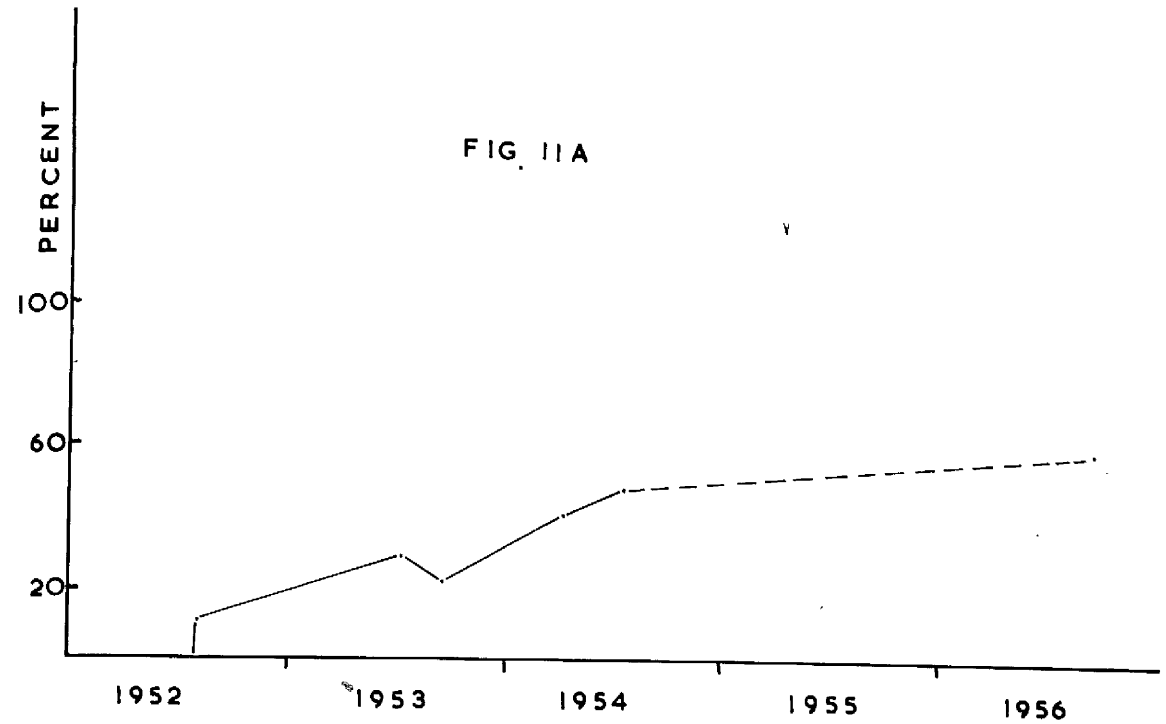

Fig. 11A: Total Basalt, Total percentage colonised.

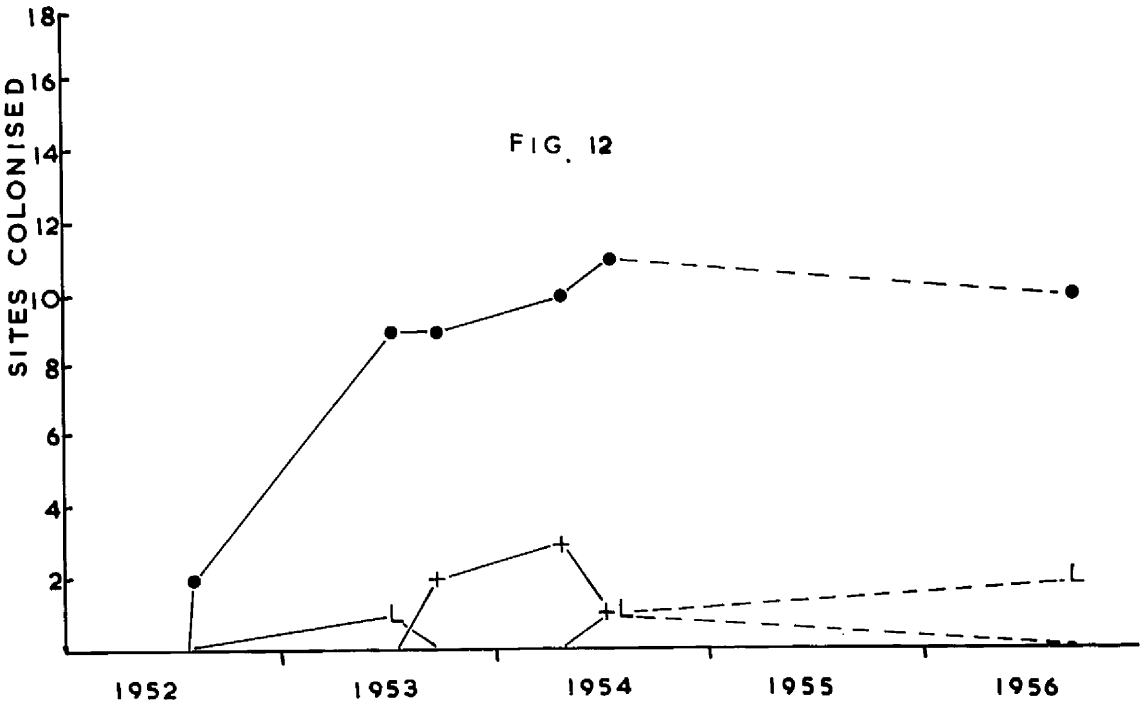

Fig. 12: Total Slate. Sites colonised by each species.

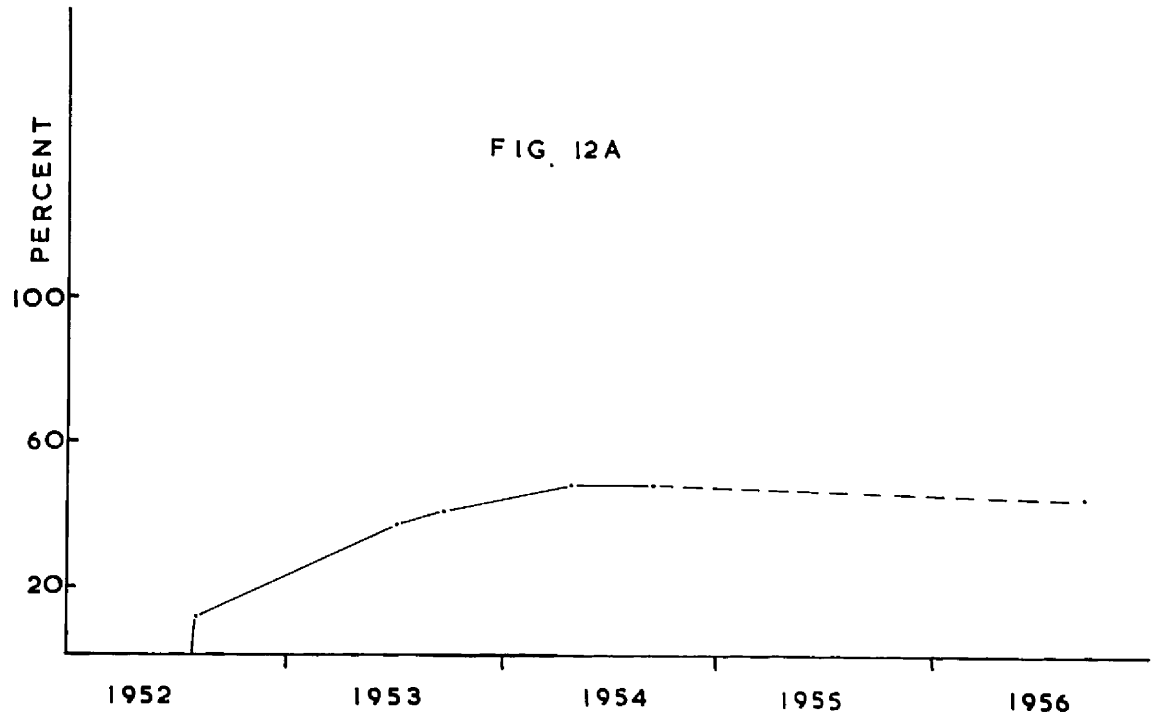

Fig. 12A: Total Slate. Total percentage colonised.

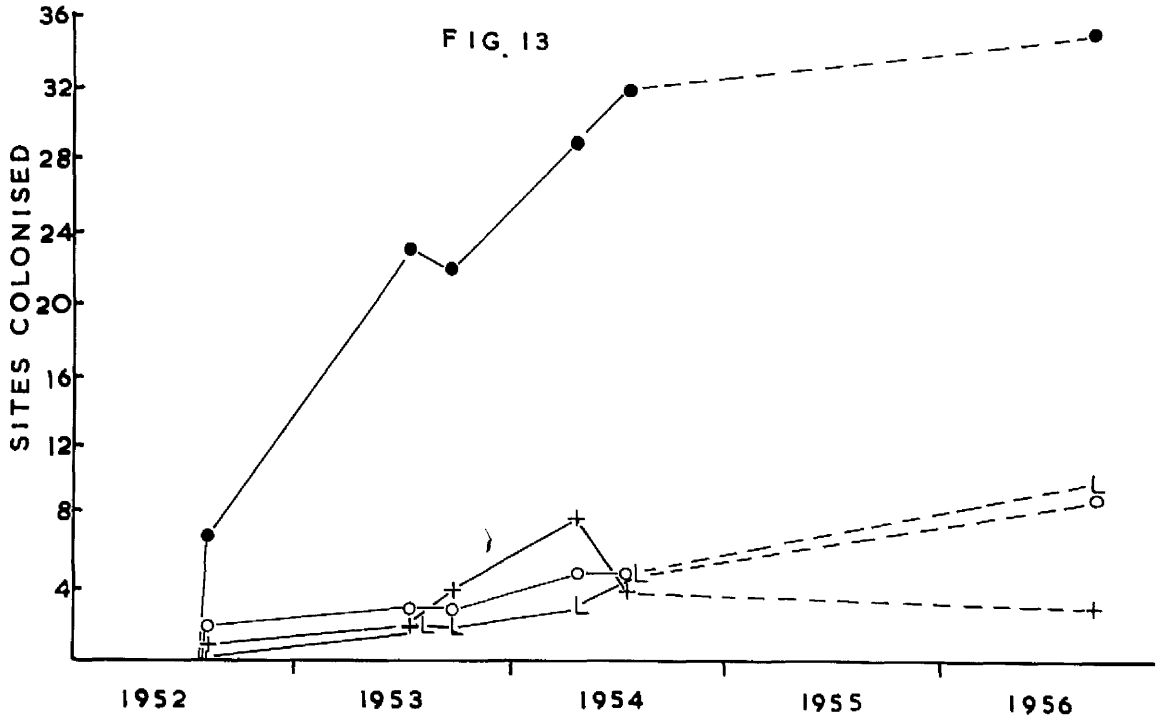

Fig. 13: Grand Total (81 units), Sites colonised by each species.

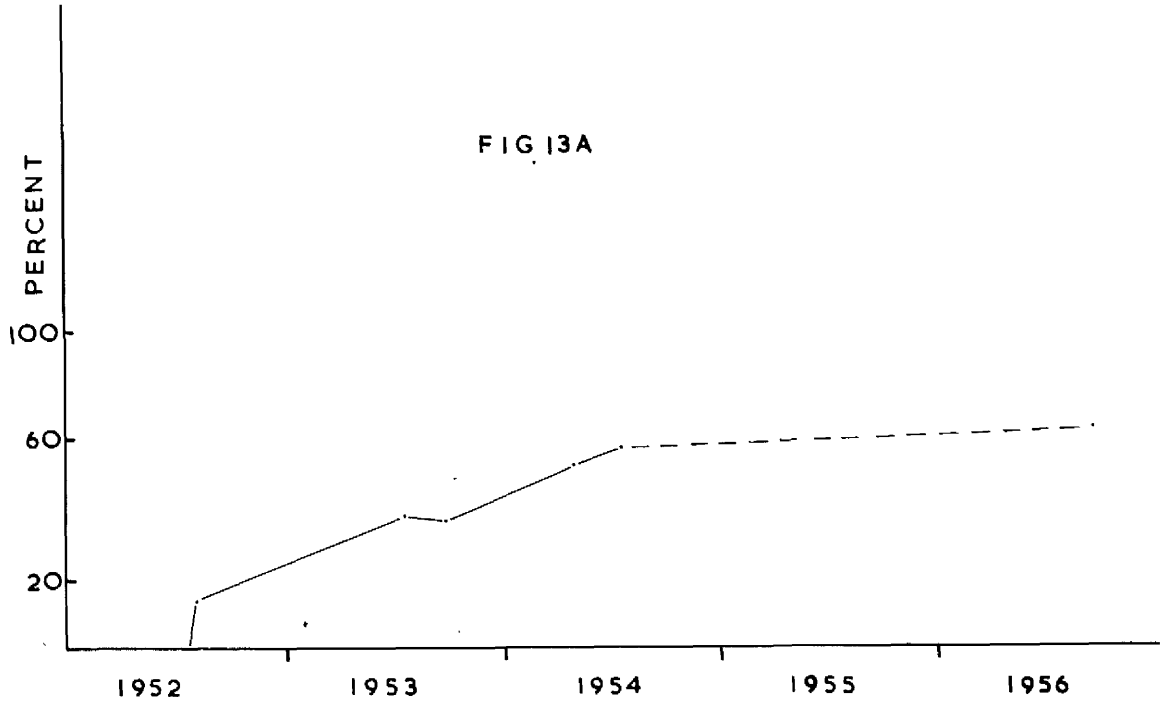

Fig. 13A: Grand Total (81 units), Total percentage colonised.

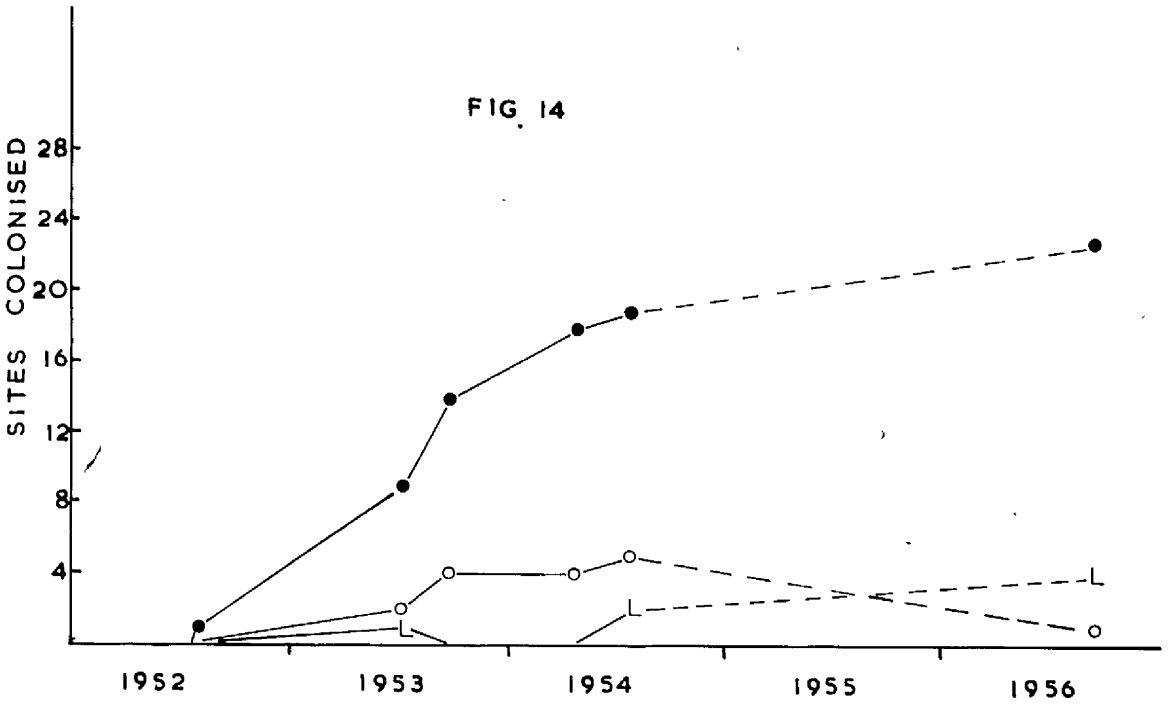

Fig. 14: Sandstone Quadrat (compact). Sites colonised by each species.

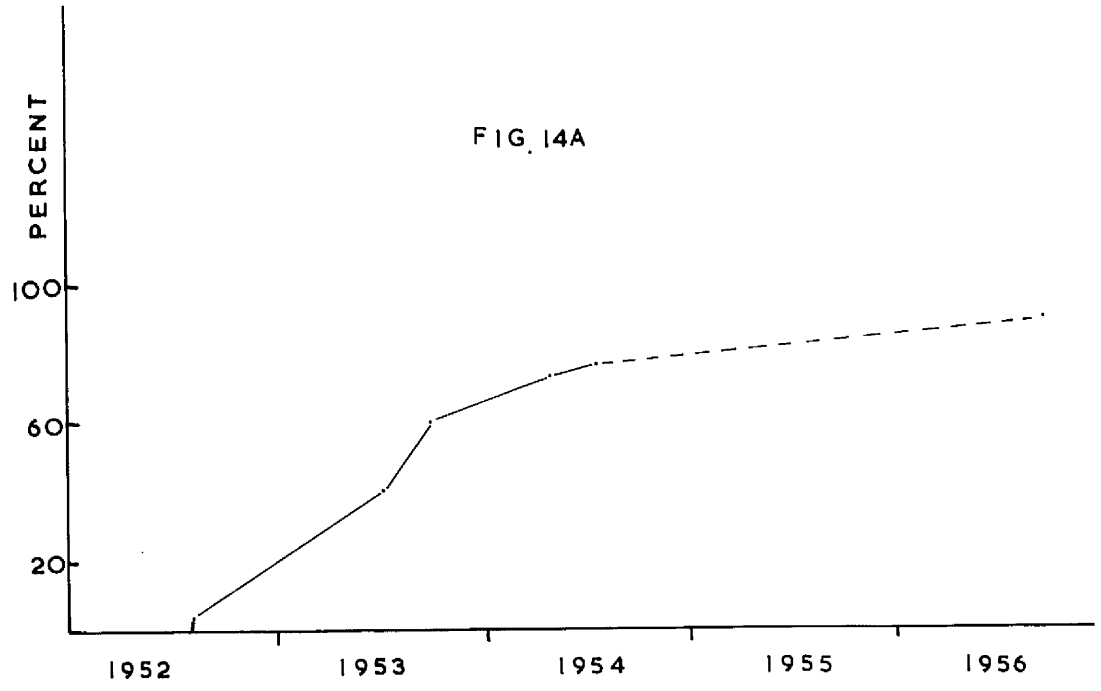

Fig. 14A: Sandstone Quadrat (compact). Total percentage colonised.

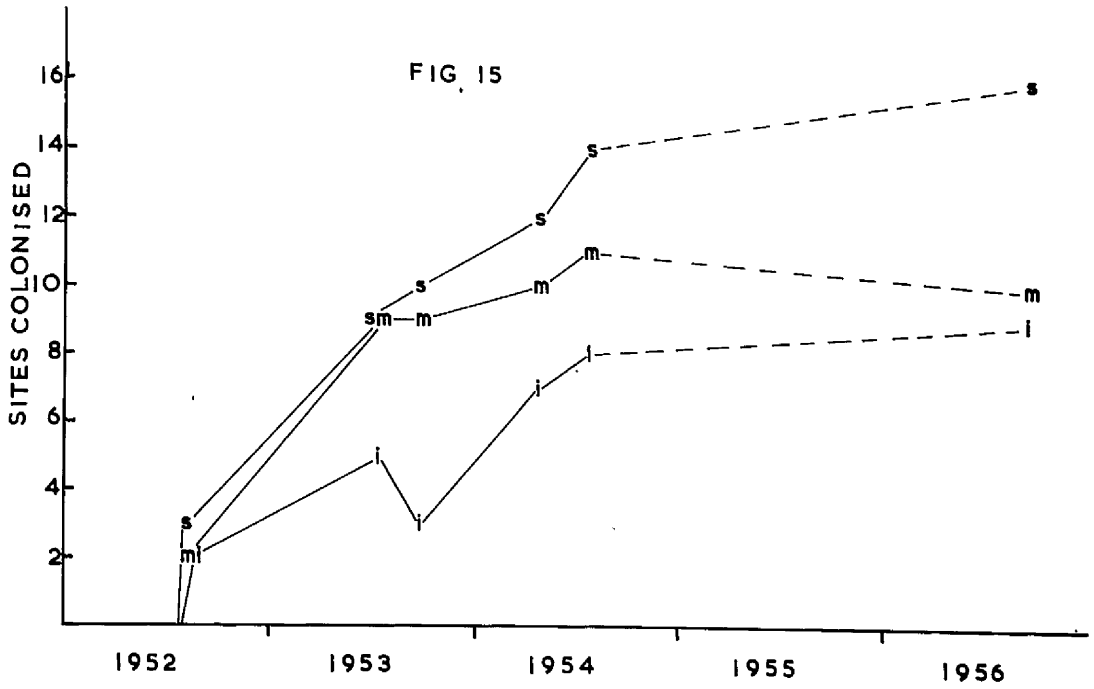

Fig. 15: F.lemani, different rock-types colonised.

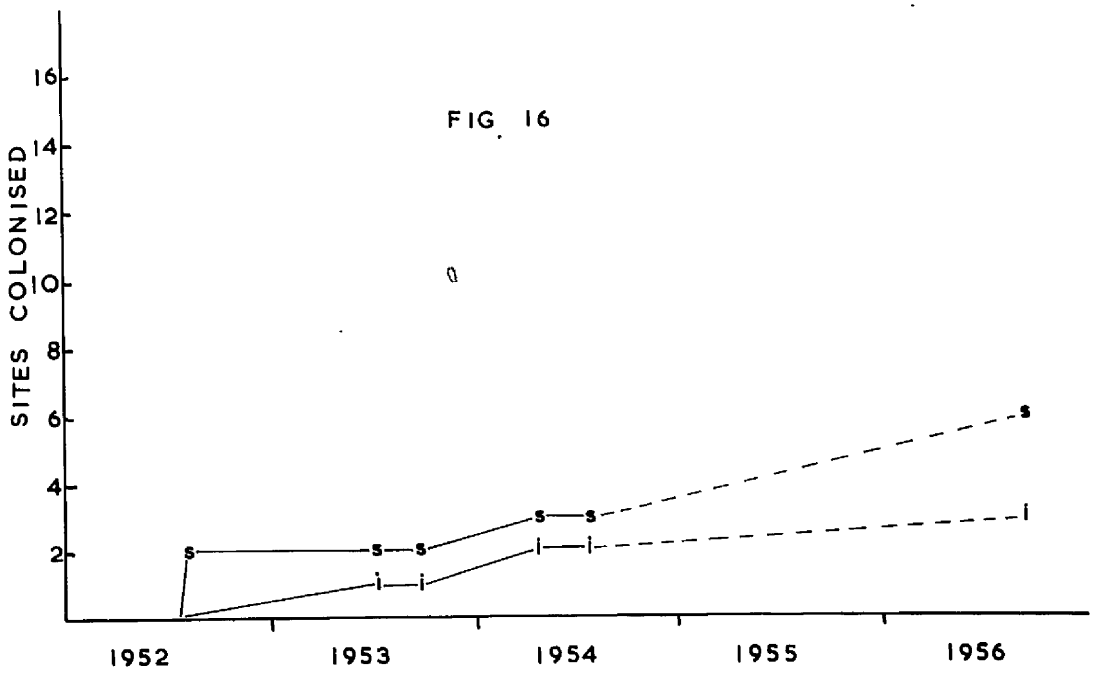

Fig. 16: M.scabrinodis, different rock-types colonised.

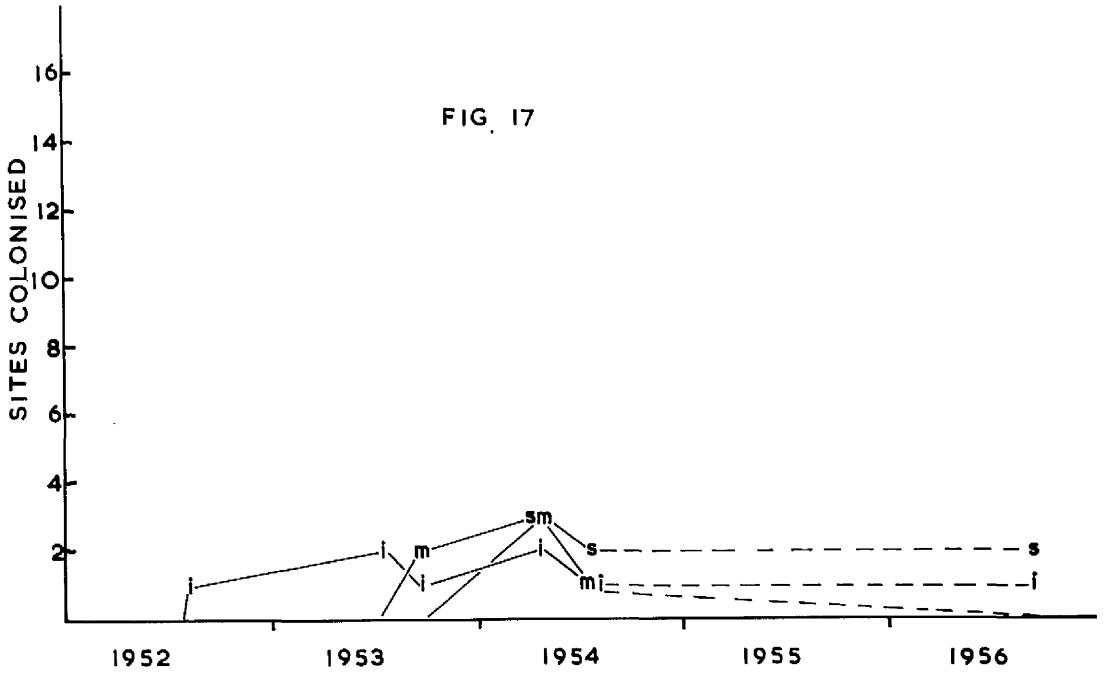

Fig. 17: H.rubra, different rock-types colonised.

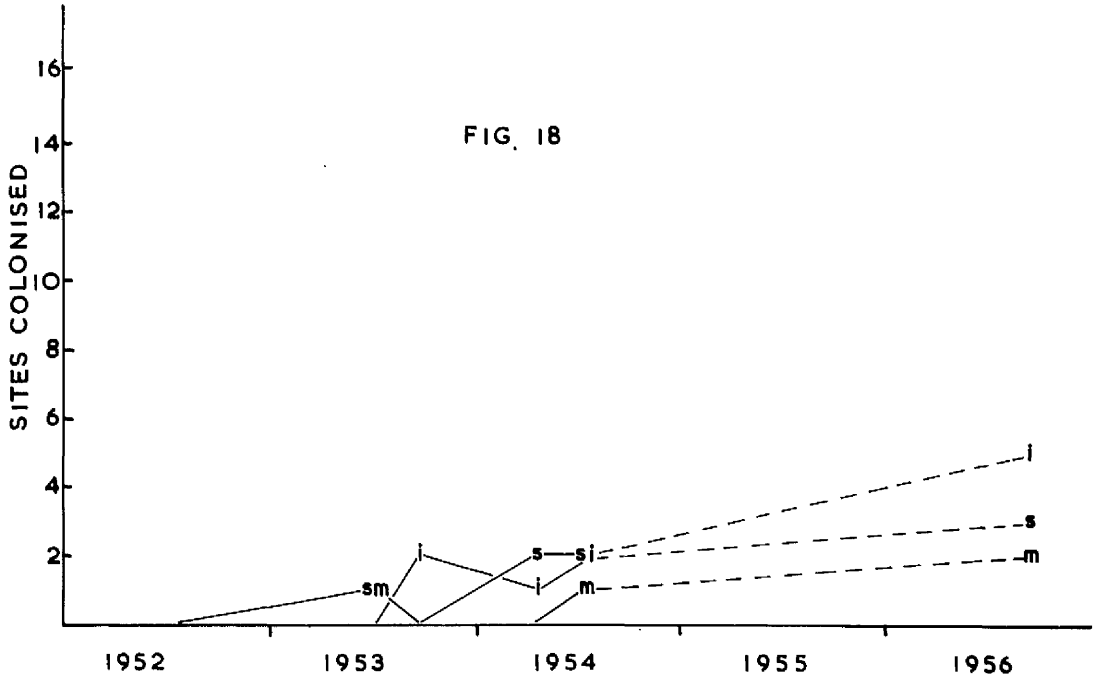

Fig. 18: L.accervorum, different rock-types colonised.

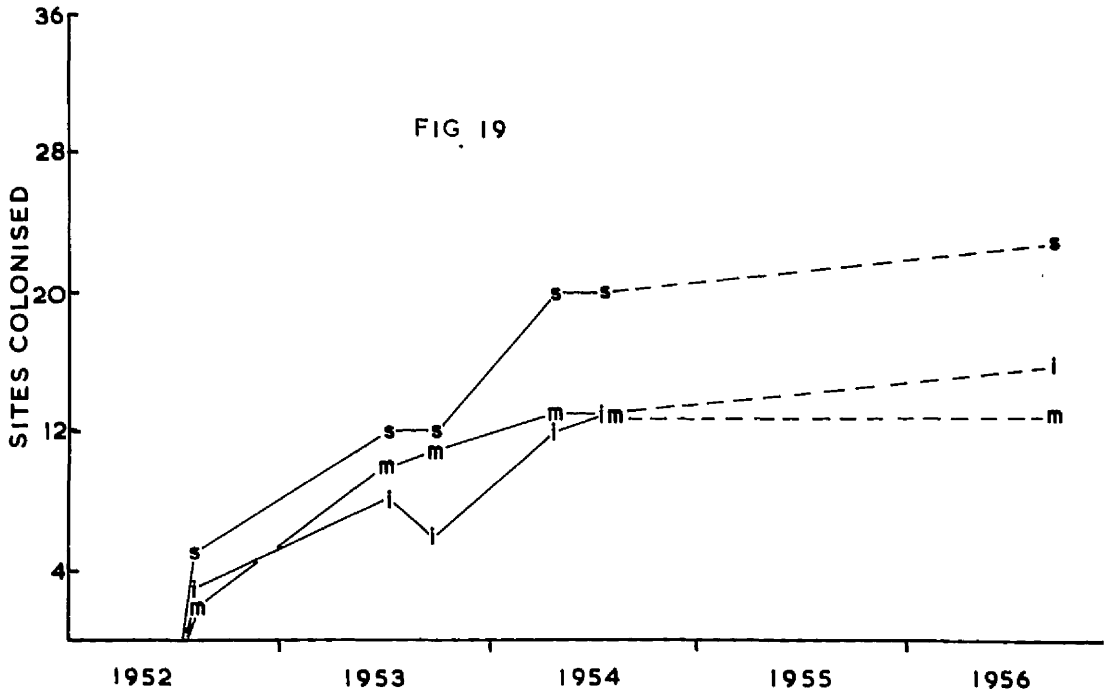

Fig. 19: Total Ant Species, different rock-types colonised.

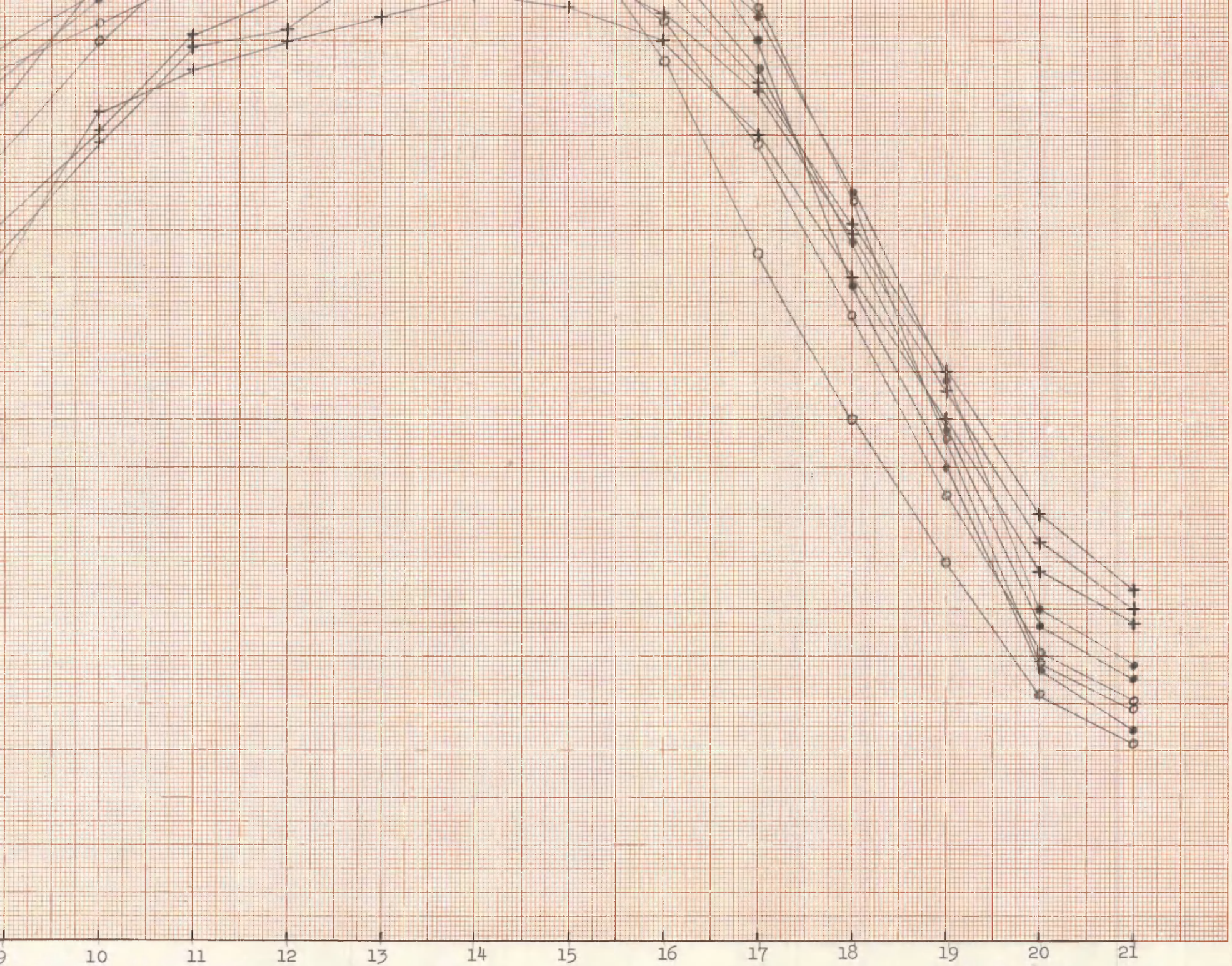
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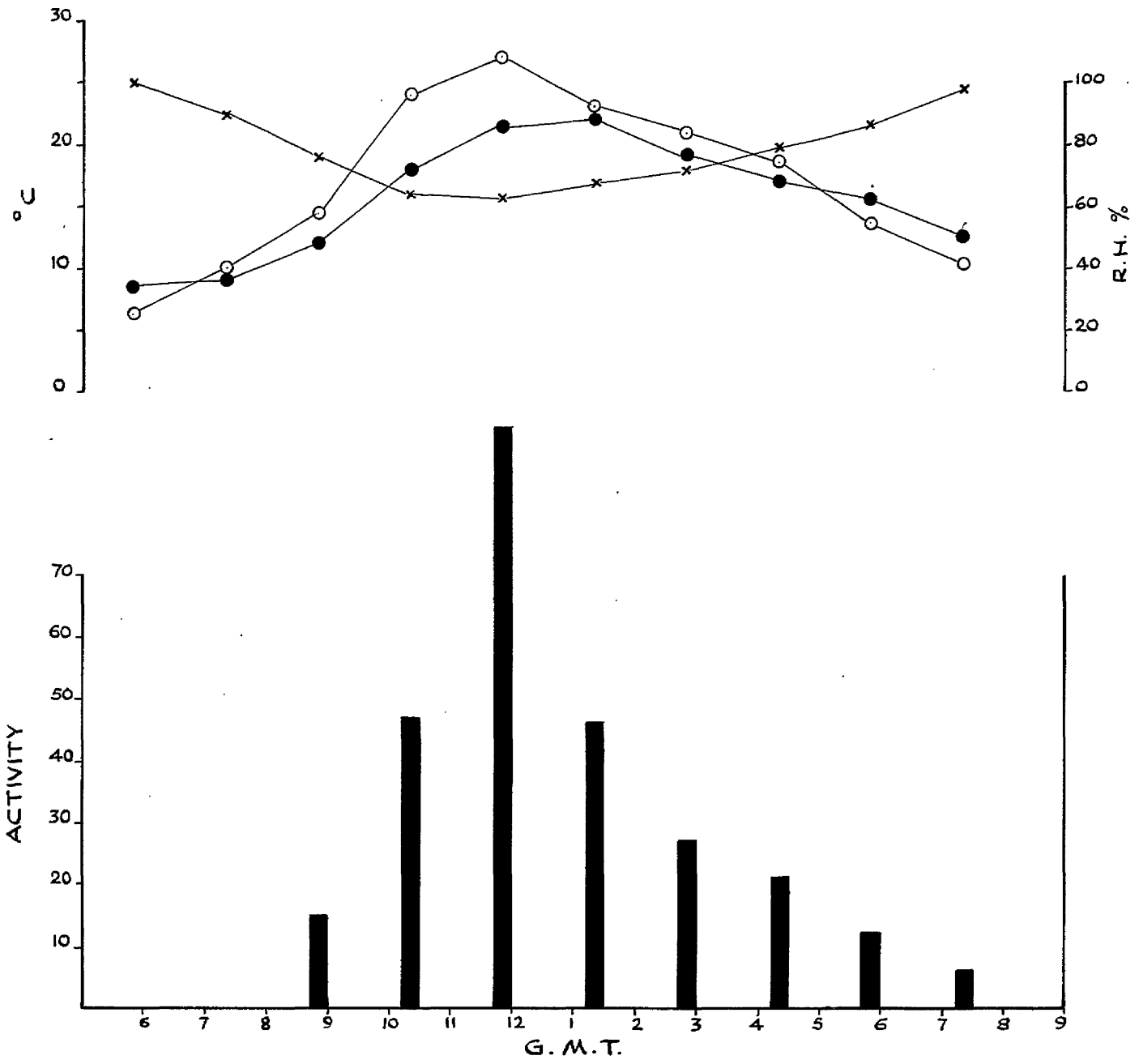
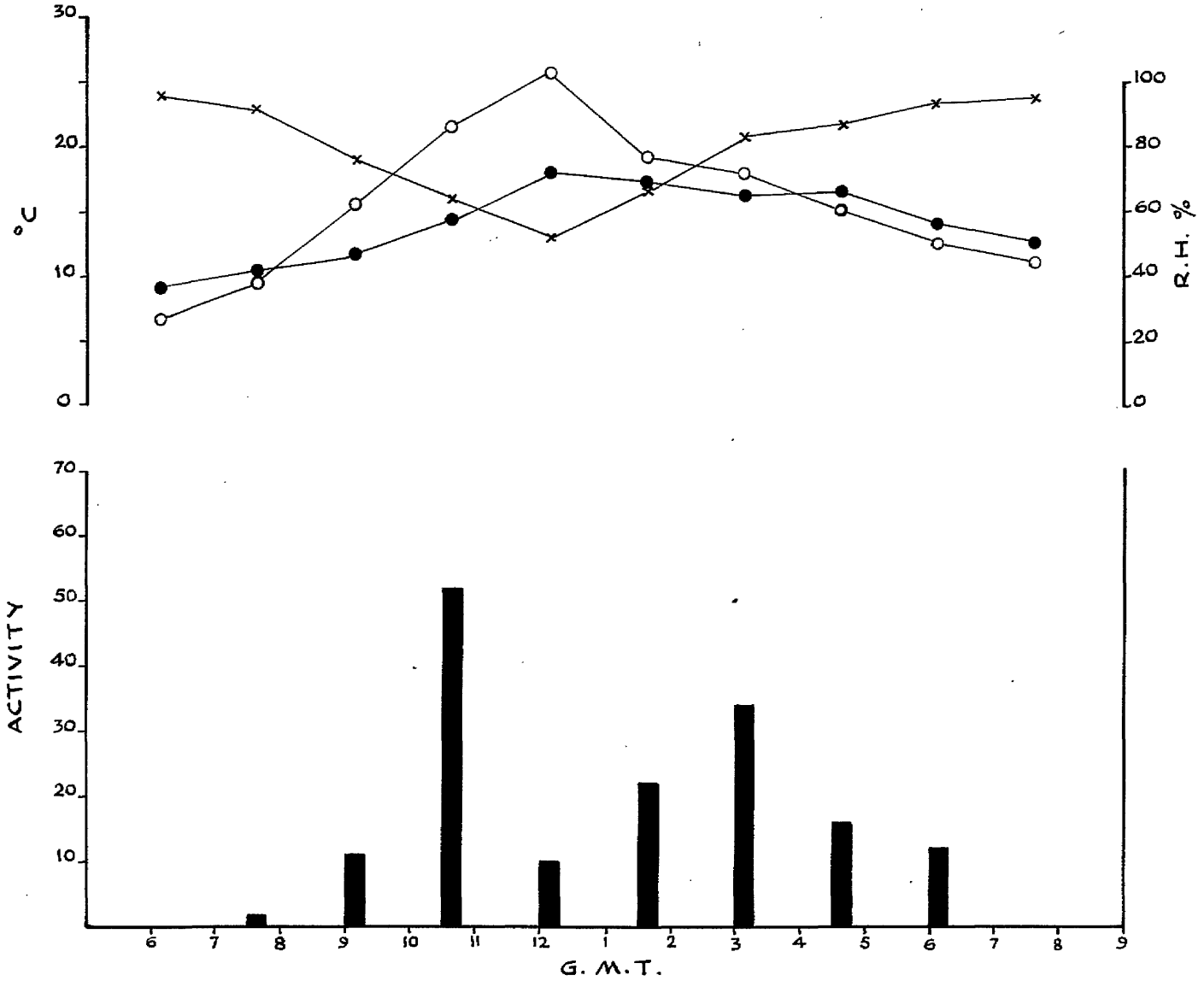
FIG. 21



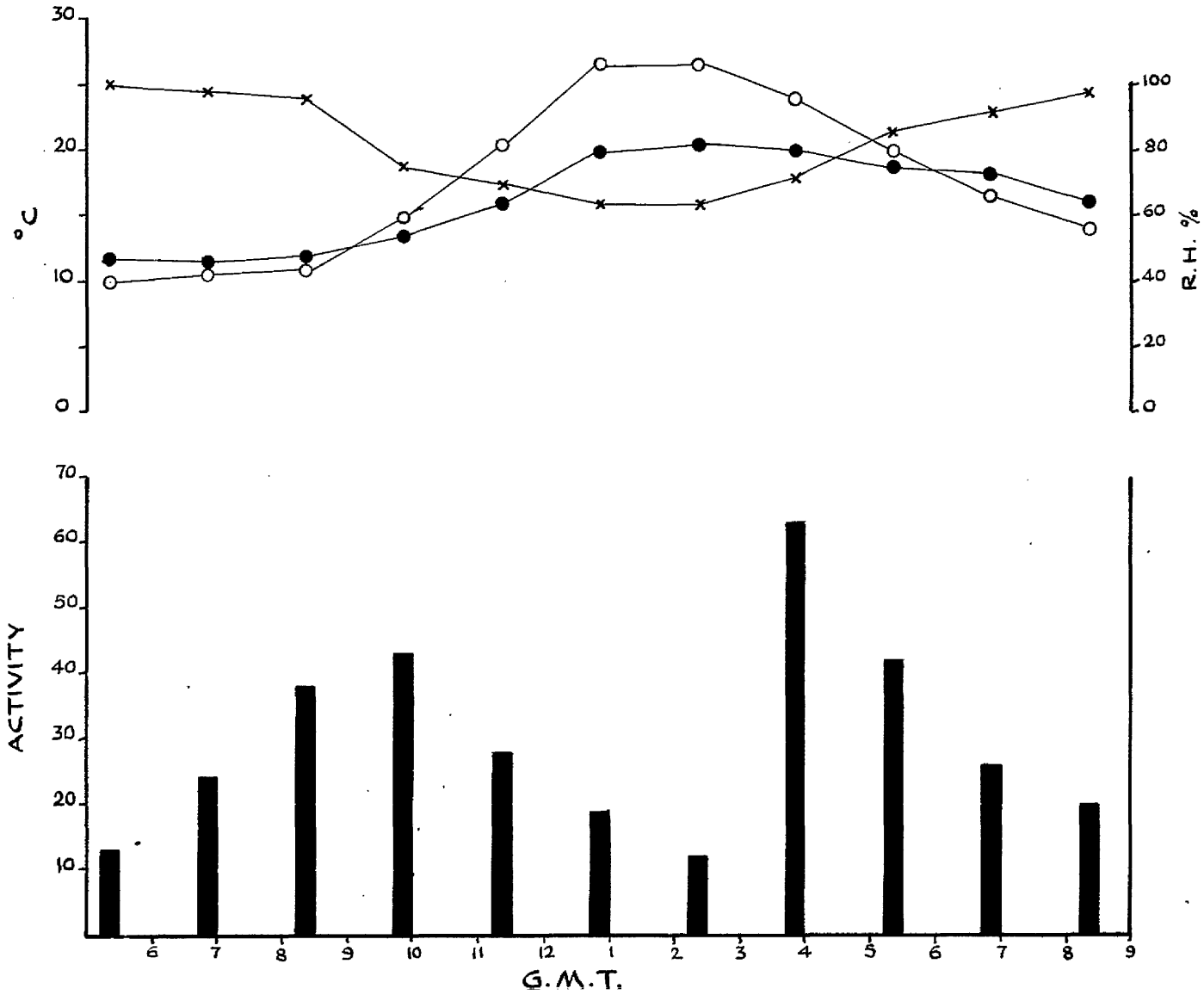
PERIODICITY OF F. IEMANI

FIG. 22.



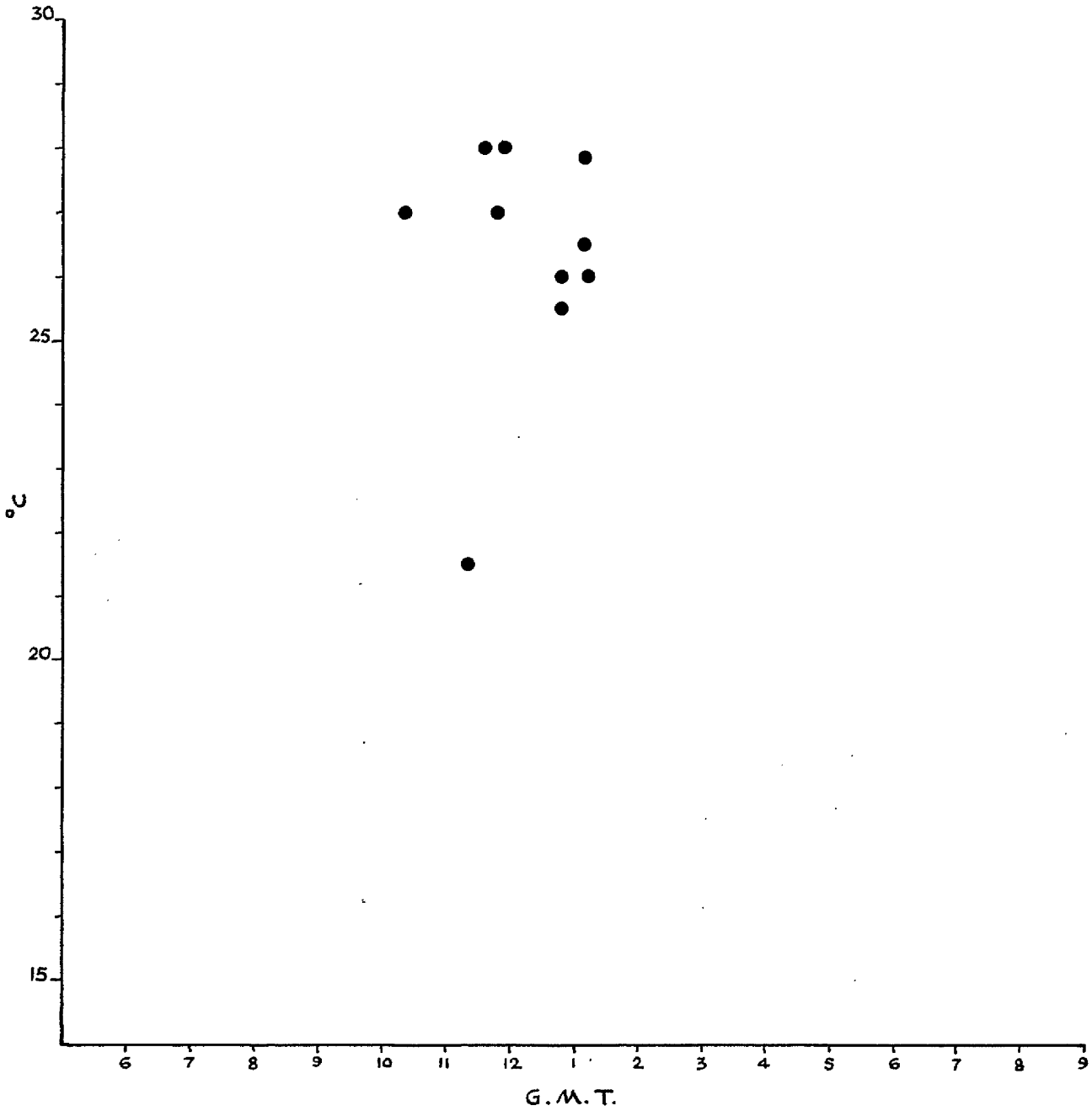
PERIODICITY OF M. SCABRINODIS

FIG. 23



PERIODICITY OF M. RUBRA

FIG. 24

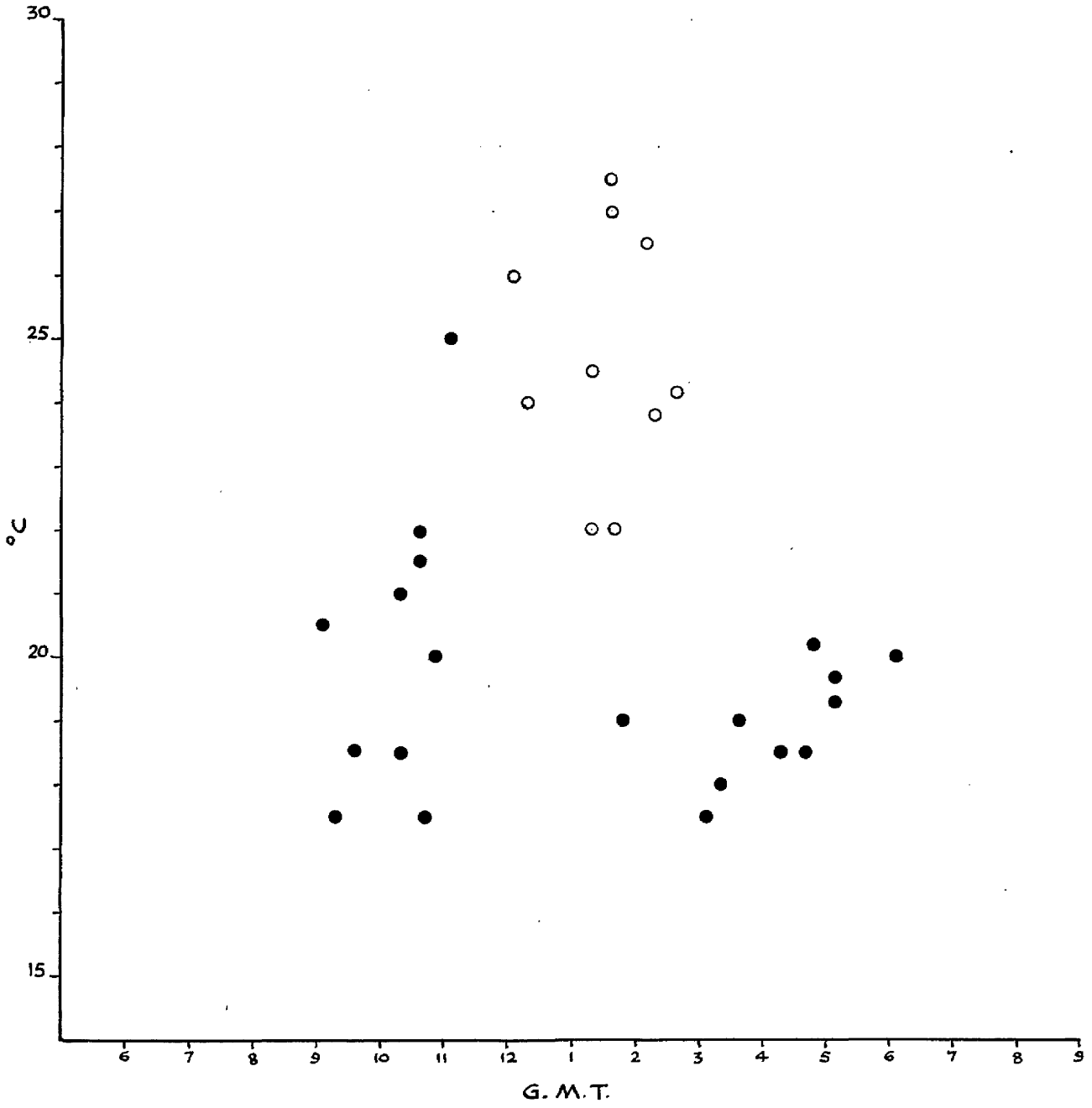


ACTIVITY MAXIMA ●

OF

F. IEMANI

FIG. 25



ACTIVITY MAXIMA ●

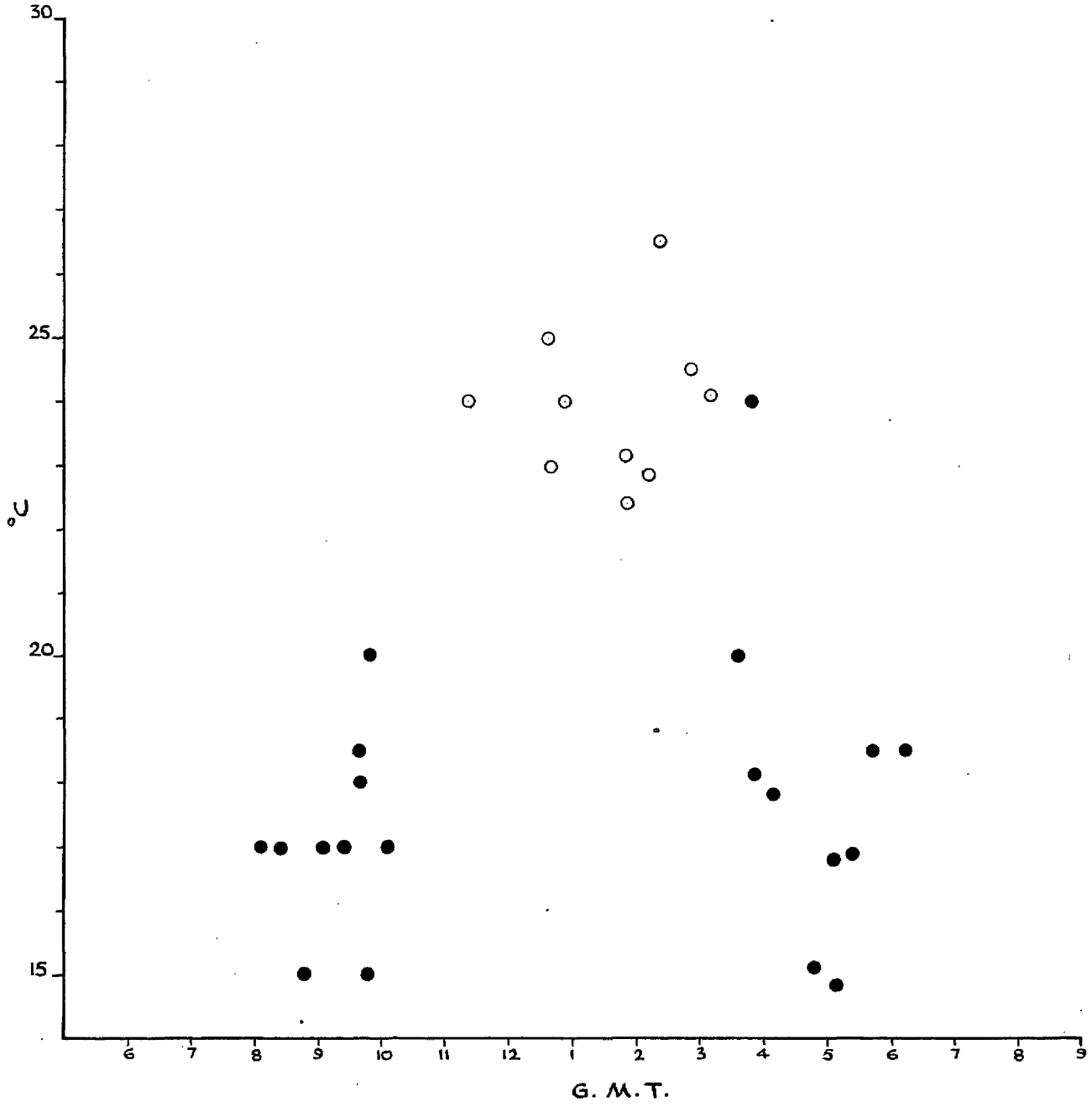
AND

MID DAY MINIMA ○

OF

M. SCABRINODIS

FIG. 26



ACTIVITY MAXIMA ●

AND

MID DAY MINIMA ○

OF

M. RUBRA

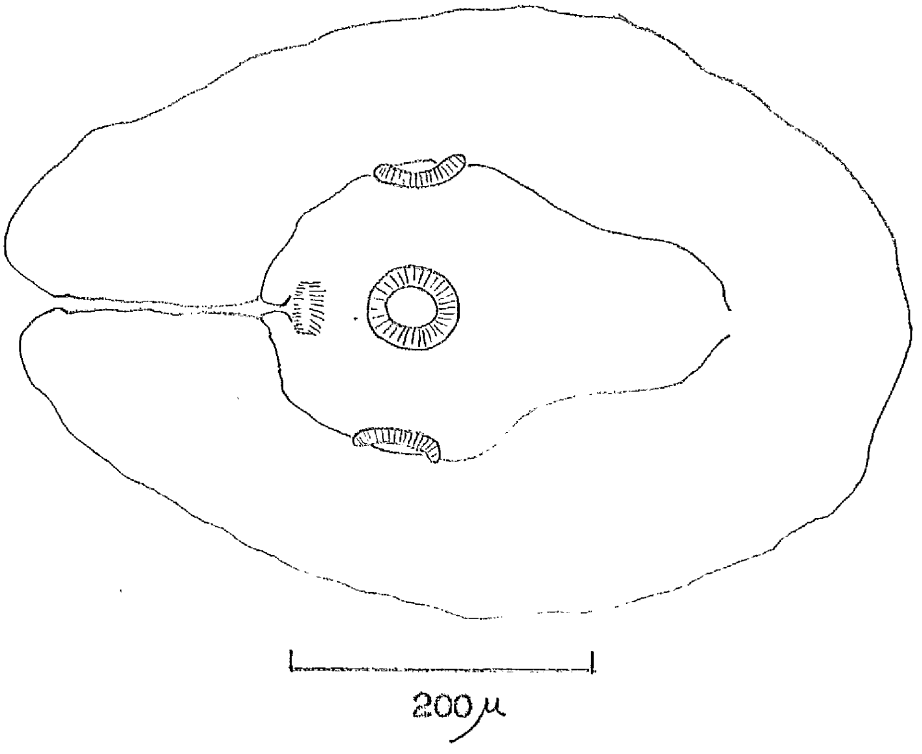


Fig. 27 Cysticercoid.

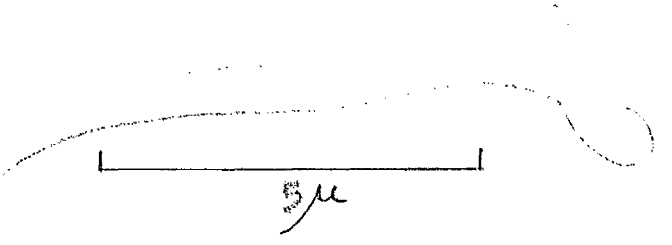


Fig. 28 Rostellar Hook.

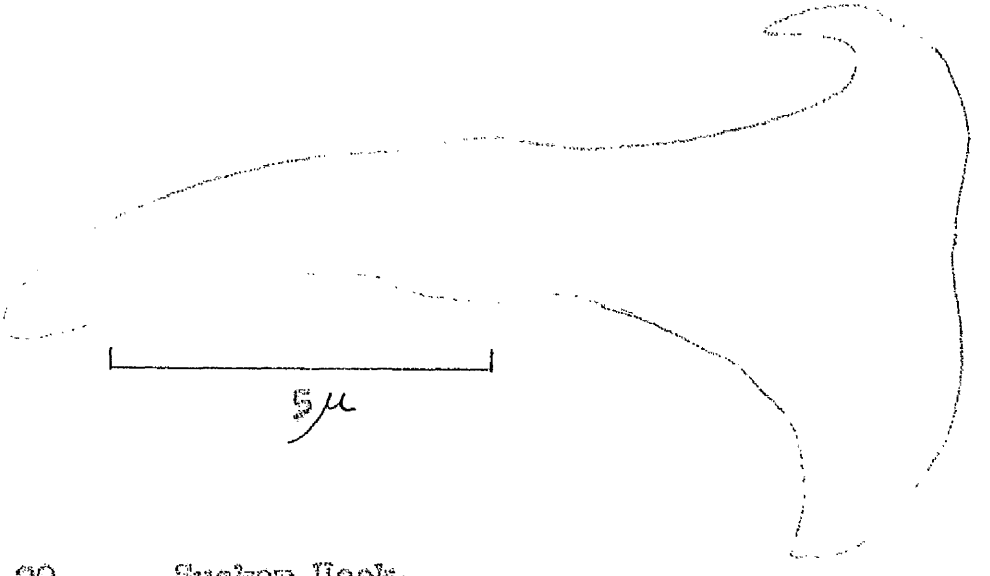


Fig. 29 Sucker Hook.

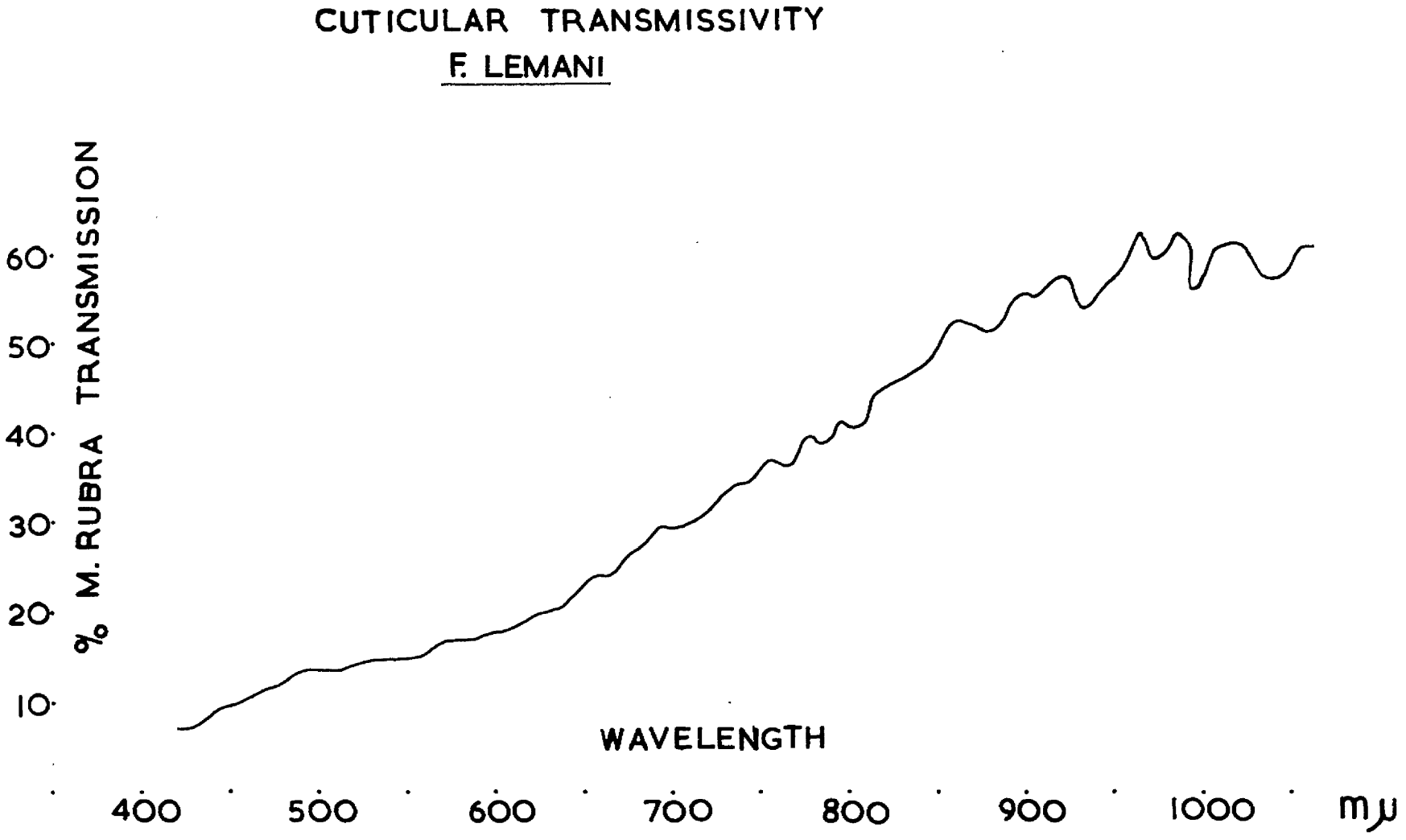


Fig. 30. Transmissivity of F. lemani cuticle compared to that of M. rubra cuticle.

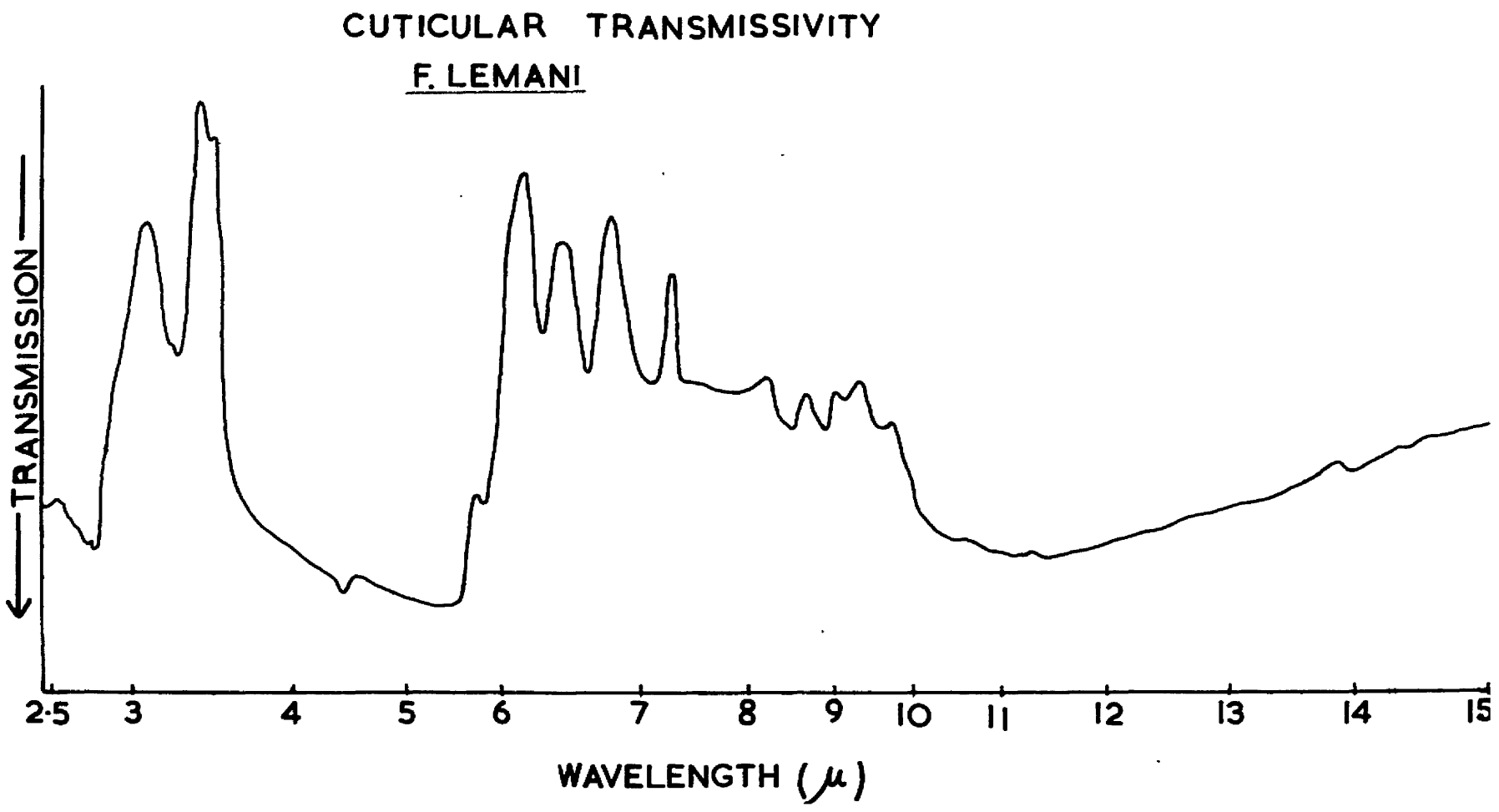


Fig. 31. Transmissivity of F.lemani cuticle in the infrared.

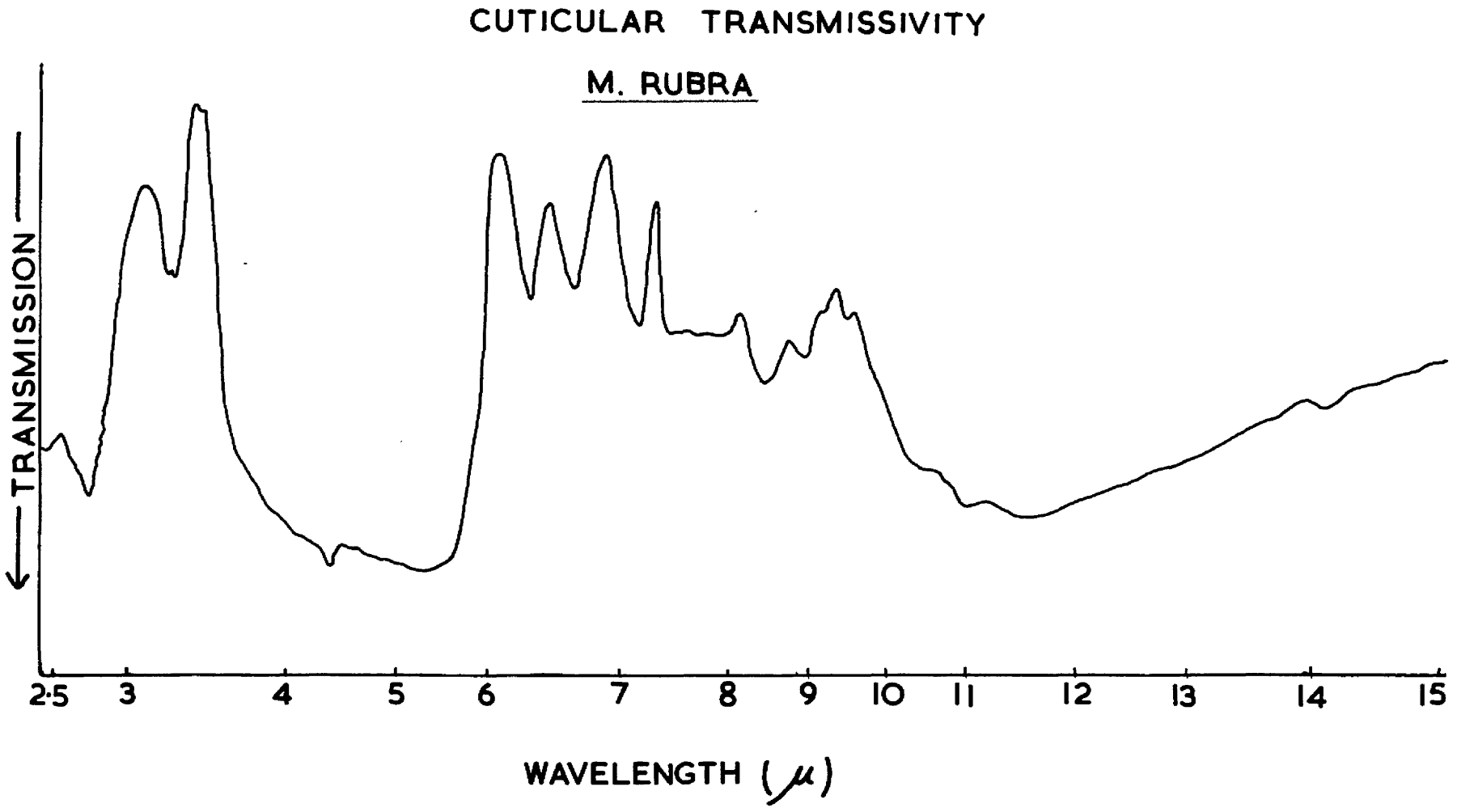


Fig. 32. Transmissivity of M.rubra cuticle in the infrared.

Fig. 33. Reflectance values of different rock-types.